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# Quaestiones entomologicae



A periodical record of entomological investigations,  
published at the Department of Entomology, Uni-  
versity of Alberta, Edmonton, Canada.





## QUAESTIONES ENTOMOLOGICAE

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### Book Reviews

DAVIS, H.S., Editor. MEILLON, BOTHA DE, HARRINGTON, J. S. and KALK, MARGARET, Associate Editors. 1964. Ecological Studies in Southern Africa. Monographiae Biologicae. Vol. XIV. Dr. W. Junk. The Hague. xxiv + 415 pp. 23 plates. 47 figs. Cloth bound. Price - 60 Guilders (\$18.00 Canadian).

This volume is intended as a companion volume to Biogeography and Ecology in Australia, vol. VIII in the same series\*. It contains 28 papers on ecological studies in southern Africa of which eight deal directly or indirectly with insects. The general intention is to make available to workers outside southern Africa a summary of ecological work being carried out there and in this it succeeds. However it does not cover all aspects of the ecology of southern Africa and so is not as useful as its companion volume on Australia.

Most of the papers are general in scope and some of them are rather superficial. Papers of especial interest are that by Cooke on the Pleistocene environment in southern Africa, two papers by Vesey-Fitzgerald and A. Leu on locusts and a paper by Brynard on the effects of veld burning on the vegetation and game in the Kruger National Park, the first scientific study I have seen of this very controversial subject. The paper by Alcock on the advance of the deserts is also of considerable interest.

An introductory chapter integrates the papers and gets them into the perspective of other research in southern Africa. Useful bibliographies accompany each paper.

The book is printed on high quality paper and has an attractive and durable dust cover. The quality of the illustrations is good and that of the photographic plates is excellent.

This book should be referred to by all persons interested in African ecology but cannot be considered worth its extremely high cost.

SMIT, BERNARD. 1964. Insects in Southern Africa : How to control them. Oxford University Press. Cape Town. South Africa, xiv + 399 pp. Price - Rand \$4. 95 (\$8. 75 Canadian).

This is a small volume written for "Students, Health Officers, Gardeners and Farmers" rather than Entomologists, by one of South Africa's most respected entomologists. The work integrates and summarizes all that is known about insect pests and their control in South Africa in a manner that can be readily understood by laymen. It is written in a friendly, breezy style laced with anecdotes from the experiences of the author and others. Technical terms are kept to a minimum and those that are necessary are explained in the text obviating the need for a glossary.

Although the book is mainly concerned with pests, beneficial insects, especially those used in biological control, receive a fair share of the space and conspicuous insects of little economic importance such as mayflies and dragonflies are not excluded.

The sections on control are refreshing at the present time, when most books on this topic tend to stress chemical controls to the exclusion of all others. One frequently finds advice against spraying when natural enemies are present and considerable weight is given to cultural controls such as proper rotational grazing and the proper timing of agricultural practices.

The older Pre World War II insecticides are also recommended when the author believes they are still adequate or superior to the newer ones.

Persons with no background in entomology may find the taxonomic arrangement of the book confusing and it may prove difficult for an untrained person to run down the source of his trouble from it. This is to some extent offset by a visual index in which figures of all major groups of insects and terrestrial arthropods are indexed to the appropriate text, but remains a major fault.

In many ways this work is a model of extension writing and although it refers exclusively to southern Africa should be read by all persons connected with entomological extension work.

Peter Graham



## EFFECTS OF MICROWAVES ON *PERIPLANETA AMERICANA* AND *TRIBOLIUM CONFUSUM*

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The cockroach, *Periplaneta americana* L. and the confused flour beetle, *Tribolium confusum* Duv. can be killed by low-level microwave power radiation at a frequency of 2,450 megacycles (mcs) with electric field strengths less than 65 volts per cm (V/cm) in a plane wave transmission system, as well as in multimode resonant cavities (electronic ovens) supplied with 1 or 2 kilowatts (kw) of power. The lethal effect of radiation at this frequency is mainly due to heat. In *P. americana*, localised internal molecular heating occurs, due to the size of the insect. With the smaller *T. confusum*, direct heating of the insect does not appear to be a predominant factor but it is shown that these insects can be killed in large volumes of flour, with microwave power used to raise the temperature of the material. However, the exposure time required depends on the insect's size in relation to the wavelength. Effects on the activity of both species were observed and adverse effects on reproduction are established with *T. confusum* adults.

### INTRODUCTION

Frings (1952), and Whitney *et al.* (1961) have discussed the effectiveness of radio frequency electromagnetic waves in killing certain insect species. Their results show that the mortality is predominantly a thermal effect, energy being absorbed by the insects in preference to surrounding media such as flour and grain. Reproduction was not affected in those specimens that survived the treatment (Whitney *et al.*, 1961).

This investigation was made to determine the effectiveness of far higher frequencies, in the radar range (2,450 mcs), at comparable incident power levels (0.5 to 2.0 kw) on the cockroach *Periplaneta americana* L. and the confused flour beetle, *Tribolium confusum* Duv.

The generation and transmission of microwave power has been described by Okress *et al.* (1964). The energy transfer systems and the thermal effects in relation to the properties of heating dielectrics have been discussed by Copson (1962) and Voss (1965). For the work described here, microwave power was generated at 2,450 mcs by a 2 kw magnetron used to power a plane wave transmission system 72 cm wide, the metal plates of which were separated by 5 cm in the direction of the electric field. In the latter case, the power density was variable between 1.25 and 5 w/cm<sup>2</sup>, measured by a calibrated power meter on the coupling system to the magnetron. A power density of 5 w/cm<sup>2</sup> corresponds to an average transverse field strength of 65 V/cm in the transmission system.

Insect and environment temperatures were measured with a needle-point iron-constantan thermocouple referenced against melting ice. Standard rearing techniques were used for both insect species.

## RESULTS

*P. americana* L.

Female roaches were placed individually in small enclosures drilled in nonpower absorbent plastic foam blocks in petri dishes, and treated in the plane wave transmission system. Various exposure times and power densities were used. After exposure, the internal body temperature was recorded in three places. Insects that survived the exposure were kept in glass observation jars and supplied with food.

It was found that an incident power density of  $1.25 \text{ w/cm}^2$  kills the insects in 90 seconds after which the average body temperature was  $60^\circ\text{C}$ ; a power level of  $5 \text{ w/cm}^2$  kills the insects in 5 seconds with a body temperature of  $72^\circ\text{C}$ . Halving the above exposure times caused the insects to be knocked down and they died within three to five days. The minimum body temperature recorded for a specimen which died at once was  $37^\circ\text{C}$ , after treatment with  $2.5 \text{ w/cm}^2$  for fifteen seconds. About 60 roaches were used in these tests. Roaches heated in a conventional oven (at  $60^\circ\text{C}$  for seven minutes) survived and behaved normally (average body temperature  $38^\circ\text{C}$ ). After twenty minutes in the same oven death resulted, with a body temperature of  $41^\circ\text{C}$ .

Although the above results are not completely determinant, it is postulated that either localised heating or other physiological changes occur within the insect at low energy densities. The problem is particularly complex as an unknown proportion of the power density incident on the insect is transmitted through it. The known behaviour of dielectrics containing water suggests that the transmitted power would increase with dielectric (insect) temperature. Further, it was found that legless specimens heat more slowly than normal ones, whereas the relative orientation of the body to the electric field had no observable effect.

*T. confusum* Duv.

Different developmental stages of the confused flour beetle were treated in a carefully designed  $48.5 \times 40 \times 38.5 \text{ cm}$  multimode cavity, excited by a magnetron at 2,450 mcs. In one test, 1.2 kw of power was supplied to ten pounds of flour in the cavity, in which different stages of the insect were confined to specimen tubes distributed uniformly throughout the volume. After 2.5 minutes a fairly uniform temperature of the flour was recorded at  $42^\circ\text{C}$  (ambient  $25^\circ\text{C}$ ). Mortality rates were zero. The same procedure was followed using 25 pounds of flour. The temperatures were recorded as  $32^\circ\text{C}$  (uniform) after 2 minutes,  $45\text{--}75^\circ\text{C}$  and  $55\text{--}90^\circ\text{C}$  after 4.5 and 7 minutes respectively, the variation of temperature being due to non-uniform heating in still flour, caused by variations in the electric field strength and moisture content (average value 12%). Specimens were removed from various areas at the times indicated. After the 4.5 minute interval, some insects survived in the lower temperature zones, all others were killed. Further tests indicated that the reproduction of *T. confusum* was affected by this treatment. In one test designed specifically to investigate this, a large number of insects, lightly covered with flour were exposed to 1.2 kw in the cavity system for 4 minutes. The initial mortality was zero but 90% failed to reproduce.

## DISCUSSION

In view of the technical feasibility of generating high levels of microwave power at low cost, the method may prove to be economically feasible for sterilizing flour infested with *T. confusum* and may have other applications. Of more fundamental interest is the possibility of isolating the thermal and physiological effects induced by high frequency electric fields using the techniques described in this paper.

## ACKNOWLEDGEMENTS

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## THE GENITALIA OF NORTH AMERICAN PENTATOMOIDEA (HEMIPTERA: HETEROPTERA)

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The male genitalia of 85 and the female genitalia of 80 species of North American pentatomoid bugs are described. The male genitalia were found to vary very widely in the tribes Pachycorini and Odontoscelini of the Scutellerinae. The female genitalia were less variable. Species in the tribe Scutellerini are very easily defined on the basis of the male genitalia. The Pentatominae, Asopinae, and Podopinae are very uniform in the structure of the genitalia and are closely related to one another. The spermatheca of all species examined in the above subfamilies except *Trichopepla semivittata* (Say) (Pentatominae), has an elongate membranous dilation with a central sclerotized rod. Median penial lobes occur only in the Pentatominae, Asopinae and Podopinae with the exception of one scutellerine, *Symphylus caribaeus* (Kirkaldy). The Cydnidae exhibit great diversity of form both in the male and female genitalia. The status of this family will remain obscure until further species have been examined. The Acanthosomidae possess pentatomine type genitalia. The genitalia of *Piezosternum subulatum* (Thunberg) do not resemble those of other species of the Tessaratomidae so far described. On the basis of this work it is suggested that the Scutellerinae be accorded family status; the Asopinae and Podopinae should be reduced to tribes within the Pentatominae; the Acanthosomidae reduced to subfamily status within the Pentatomidae and *Piezosternum* should be raised to subfamily status within the Tessaratomidae. Phylogenetically the Pentatomoidea show some relationship to the lygaeoid group, but this relationship is not close. The two groups are probably derived from a common ancestor. The Tessaratomidae are an early offshoot of the hypothetical pentatomoid ancestor. The main stock then developed into the Scutelleridae and the Pentatomidae with the Acanthosominae a very early offshoot of the latter group.

### INTRODUCTION

This study was undertaken with the hope of showing more clearly the interrelationships of the North American genera of the Pentatomoidea. Though many more problems have been raised than solved, I hope that some basis is provided for a thorough taxonomic revision of this group in the future. Both the male and female genitalia provide good taxonomic characters and they will no doubt be used with increasing frequency, especially where large numbers of characters are required for analytical purposes as in the rapidly developing field of numerical taxonomy.

Fairly detailed descriptions have been made of the male genitalia while the female genitalia have been treated rather more generally. A discussion of the results in each section of the work has been given with a final overall synthesis of all points raised. The classification I have proposed cannot be regarded as final any more than any other classification, but, in general, it supports accepted classifications. A satisfactory classification will depend on a thorough analysis of this superfamily on a world-wide basis.

### MATERIALS AND METHODS

The specimens used in this work were selected from dried museum material; males of 85 species and females of 80 species of pentatomoid bugs were studied and a total of 256 specimens were examined. Representatives of the type species of each genus were chosen wherever possible. Material dissected out of each specimen has been placed in a microvial and attached under the specimen. All material has been returned to the United States National Museum, Washington.

The genitalia were studied after treatment with 10% KOH in the usual way. The terminalia were cleared in polyvinyl lactophenol, methyl salicylate, or glycerine. Wherever necessary, chlorazol black was used as a stain for membraneous structures. In some cases the internal structure of the vesica could only be studied after thorough bleaching in chlorine (McDonald 1961). A technique described by Kumar (1964) was used to check the connections of the internal ducts of the vesica. This method was not found to be entirely satisfactory.

Transverse sections of the vesica of *Lamprolicra senator* (Fabricius) and *Cantao parentum* (White) were made. The vesica was embedded in paraplast, sectioned at 6 $\mu$ , stained in Mallory's triple stain and mounted in Canada balsam.

Observations were made with a Wild and a Leitz stereoscopic microscope with magnifications of up to 50X and 150X respectively. Diagrams were drawn to scale using a squared ocular grid and squared paper. Stippling where used indicates sclerotization. The conjunctival appendages have been numbered in sequence from the dorsal to ventral surface; the third are thus always ventral in position. The diagrams of the vesica have nearly all been orientated so that the seminal duct is ventral.

The classification of the Pentatomoidea throughout the descriptions and discussion sections follows that of Leston (1953c). The keys are arranged according to the proposed classification I have set out on page 68. The generic and specific names followed are those of Van Duzee (1917), with Kirkaldy (1909) as a second source of reference.

## TERMINOLOGY

### *Male genitalia*

The basic nomenclature used is that of Pruthi (1925) with slight modifications. I have retained the term median penal lobe used by Baker (1934) for the inner sclerotized lobes surrounding the vesica in Pentatominae, Asopinae and Podopinae. The homology of these lobes is uncertain. The term endophallic duct is used for the duct between the ejaculatory line which I used wrongly in previous papers (McDonald 1961, 1963). I feel this is a more basic term than conducting canal 2 of Kumar (1964). I also cannot accept the latter author's term conducting chamber in place of ejaculatory reservoir, because outside the highly specialized Scutellerini this chamber is usually well developed and probably does act as a reservoir for sperm. Figure 1 is a general diagram showing the terminology used in this paper.

### *Female genitalia*

The nomenclature used in this section is that of Scudder (1959) and Pendergrast (1957) for the spermatheca. For the purposes of this study the spermatheca has been considered as part of the female genitalia.



## MORPHOLOGY OF THE MALE GENITALIA

The external features of the male genitalia are easily observed. The appendages of the aedoeagus are sometimes difficult to expand and wherever these have not been fully expanded this is stated in the text.

The male genitalia are situated in the ninth segment which is modified into a cup-like structure, the pygophore (fig. 4). Within the pygophore is a pair of hook-like structures, the claspers (fig. 5) and a tube-like structure, the proctiger bearing distally the anus. Lying beneath the proctiger is the aedoeagus (fig. 1) attached by means of the basal plate to the ventral surface of the pygophore.

The internal structure of the vesica has been worked out and drawn as accurately as possible. However, without actually sectioning the specimens interpretation of the internal ducts is subject to error and cannot be regarded as final until sections of all species have been made. Even so, the gross morphological details are quite readily observable and these serve adequately for studies in homologies between genera at a tribal level and above.

The tribe Scutellerini, represented in North America by the genus *Augocoris* has a peculiarly developed convoluted duct passing back from the entrance of the seminal duct into the ejaculatory reservoir (fig. 83). Kumar (1964) states that this duct (conducting canal 1) is composed of two sets of canals and that the seminal duct passes directly into this duct. Cross sections of *Lampromicra senator* and *Cantao parentum* (Australian scutellerines) show quite clearly that this duct is in fact single but of a highly convoluted nature (fig. 3). Sections also show that the seminal duct opens into the base of the endophallic duct as does the convoluted duct. Unfortunately, sections could not be made of the genitalia of *Augocoris gomesii* as very few specimens were available for study.

**Pentatomidae - Scutellerinae***Odontoscelini**Fokkeria producta* (Van Duzee), 1904

Pygophore (fig. 4) with dorsal border deeply and evenly arched; ventral border U-shaped. Pygophoral opening with wide dorsal and lateral flanges. A number of small setae on dorsal and lateral borders.

Claspers (fig. 5) small stem basally wide; apically narrowing into a shallow hook; inner margin finely serrate. A number of setae on mid region of stem.

Theca (fig. 6) conical, not heavily sclerotized. Three pairs of conjunctival appendages borne on a common membraneous base: first, conical, membraneous with a small sclerotized apex; second bifid, consisting of two heavily sclerotized horns borne on a short membraneous base; third large oblong structures bluntly rounded apically, heavily sclerotized throughout and covered with numerous flat, blunt teeth.

Vesica strap-like, dorsoventrally compressed, base wide, sclerotized, fused to ventral margin of theca, tapering distally, apex membraneous and bent through 90°. Seminal duct (fig. 7) leading into a small

globose ejaculatory reservoir, walls of latter thickened; endophallic duct connected to anterior end of reservoir, apically terminating within membranous apex of vesica.

*Euitychodera corrugata* (Van Duzee), 1904

Pygophore small (fig. 8), opening with dorsal and lateral flanges, ventral border emarginate, a number of small setae scattered along the lateral margins.

Claspers (fig. 9) shallow hooks, no differentiation between apical hook and stem. A number of stout setae along stem, inner basal margin bearing many minute spines. Dorsal surface of hook scalloped.

Theca (fig. 10) small, conical. Three pairs of conjunctival appendages: first basally wide, membranous, apically produced into heavily sclerotized points; second consisting of heavily sclerotized curved horns attached to a short membranous base fused to common base; third, (figs. 10, 11) large, sclerotized plate-like structures, outer surface covered with numerous short stout spines; appendages normally folded within common base beneath second conjunctival appendages.

Vesica (fig. 10) narrow and flattened dorso-ventrally, basally attached to theca; sclerotized except for apical third. Seminal duct (fig. 12) leading ventrally into anterior portion of bilobed ejaculatory reservoir. Posterior lobe forming a small chamber lying somewhat on top of larger anterior chamber. A wide endophallic duct connecting with ejaculatory reservoir, apical opening membranous.

These genitalia resemble very closely those of *Fokkeria producta* especially in the form of the conjunctival appendages. I think that *Euitychodera* is probably congeneric with *Fokkeria*.

*Vanduzeeina balli* (Van Duzee), 1905

Pygophoral opening with a large flattened flange (fig. 13) laterally on each side; dorsal margin wide; ventral margin narrow, flattened, bearing a number of small fine setae. Proctiger with numerous long fine setae on apex.

Claspers, scythe-like (fig. 14); stem continuous with apical hook and covered with stout setae along outer margin; a number of longer setae found at base of hook.

Theca (fig. 15) small, conical, not heavily sclerotized. Three pairs of conjunctival appendages (fig. 16) present, fused onto wide membranous conjunctiva: first, basally membranous and wide; apically produced into a small curved heavily sclerotized point, second completely enclosed by their membranous common base within theca when not expanded; apex of each appendage terminating in a very large flattened, heavily sclerotized horn; third, minute structures situated at bases of second conjunctival appendages; apically sclerotized and pointed.

Vesica, small narrow and flattened, basally sclerotized and fused to conjunctiva; medianly divided into two rounded sclerotized projections lying one on each side (fig. 17) of a membranous tube, within which is the endophallic duct, projections bearing a number of teeth on their apices. Apex of vesica with a wide flange. Internally, seminal duct

passing ventrally up base of vesica and into small trilobed ejaculatory reservoir; endophallic duct straight, basally merging into apex of reservoir.

*Phimodera binotata* ( *P. torpida* ) (Say), 1824

Pygophore with dorsal margin (fig. 18) very broad, covered with fine setae; two small spine-like projections found laterally one on either side on ventral border above bases of claspers. Ventral border bearing numerous short stout setae.

Claspers (fig. 19) small, stem drawn out into a blunt apex; a square projection lying below apex forming a shallow hook. Twelve to seventeen setae found along apical half of stem; a number of very minute setae found on under surface of apex.

Theca (fig. 20) cylindrical, apical margin merging into conjunctiva when latter fully expanded. One pair of membranous cylindrical conjunctival appendages (fig. 22) attached ventrally into base of endophallic duct; a ventral canal leads back into a large ejaculatory reservoir from which a second dorsal canal opens into base of endophallic duct; latter basally thickened and thrown into a number of loops, finally widening and opening at secondary gonopore.

*Eurygastrini*

*Eurygaster alternata* (Say), 1828

Pygophore with dorso-lateral border (fig. 23) rounded, extending down on each side to fuse with flattened and plate-like ventral margin. Fine setae along margins of dorso-lateral border.

Claspers T-shaped (fig. 24) with a thick stem tapering basad. A number of fine scallopings found on inner surface of each arm of cross-piece and several small setae on each side of stem at its junction with cross arm.

Theca conical, very slightly sclerotized, bearing on the ventral margin centrally a long cylindrical membranous process (fig. 25), apex slightly sclerotized, pointed. Three pairs of conjunctival appendages present: first membranous basally, apically sclerotized forming a stout curved horn; second heavily sclerotized, horn-like; third, very small sclerotized horns.

Vesica, consisting of a long cylindrical tube, apically membranous, hook-shaped, upper margin of hook bearing a fringe of hairs; basally sclerotized and bearing on dorsal surface a pair of leaf-like vesical processes (fig. 26). Seminal duct opening ventrally into an anterior sinus to which posteriorly is attached a small elongate and heavily sclerotized reservoir. Endophallic duct originating from anterior sinus and terminating in a wide membranous secondary gonopore lying within invaginated apex of vesica.



*Pachycorini**Camirus moestus* (Stål), 1862

Dorsal border of pygophore evenly arched (fig. 27), laterally with two rounded prominences, ventral border almost straight.

Claspers (fig. 28) simple hook-like, shallow, stem fairly long.

Theca squat, cylindrical, not heavily sclerotized. Two pairs of conjunctival appendages: first (fig. 29) entirely membranous bag-like, apically rounded; second bifid, ventral arm short, flat, sclerotized and disc-like; dorsal arm membranous, cylindrical, tapering apically to a blunt point; both arms borne on a common partially sclerotized stem.

Vesica (fig. 30), complex; endophallic duct apically surrounded by a large oblong membranous sheath covered with very fine spines. Seminal duct very fine, passing ventrally into base of ejaculatory duct. A wide thickened convoluted duct extending back from entrance of seminal duct, widening posteriorly into a large sinus; latter communicating by means of a valve-like arrangement with a large dorsal ejaculatory reservoir. A long funnel-like duct connecting ejaculatory reservoir with a narrow ventral chamber latter leading anteriorly into a short endophallic duct. The vesica resembles that found in the Scutellerini (McDonald, (1964) particularly in possessing a long convoluted duct.

*Pachychoris torridus* (Scopoli), 1772

Previously described by Kumar (1965). Pygophore with dorsal margin membranous, bearing medianly a narrow, heavily sclerotized band produced into a broad median process (fig. 32), apically acute. A pair of cylindrical pygophoral appendages lying one on either side of median process; each appendage apically with two spines (fig. 33) outermost spine being single, innermost bifid. Lateral margins of pygophore somewhat flattened; ventral border flattened and shelf-like.

Claspers (fig. 34) small; stem short, stout, merging into a broad flattened hook; a number of fine setae at base of hook.

Theca (fig. 35) cone-shaped. Two pairs of conjunctival appendages: first, large completely sclerotized, horn-like structures fused to margin of theca; second cylindrical, rodlike, apically smoothly rounded bearing half way along ventral margin a stout spine, below which is a deep notch.

Vesica (fig. 36) extremely small and simple in construction; lying between bases of second conjunctival appendages; apically opening into a longitudinal groove. Seminal duct opening into a small tube expanded medianly into an anterior sinus, narrowing distally into a very short endophallic duct. The vesica is unusual in not possessing a free apical portion as in other Scutellerinae.

*Chelysomidea guttata* (Herrich-Schaeffer), 1839

Dorsal border of pygophore (fig. 37) arcuate; practically obsolete medianly, laterally produced on each side into a stout sclerotized point. Ventral margin flattened, border almost straight. Proctiger very distinct, membranous except for a narrow dorsal median sclerite apically



produced into a short curved median spine, lateral margins each produced into a long spine; anal opening lying between this triad of spines. A narrow band of very fine spicules on lateral margins on each side from base of lateral spine.

Claspers scythe-shaped (fig. 38), stem broad, a number of very small teeth found along inner margin of hook.

Theca (fig. 39) membranous, hardly differentiated from conjunctiva. Two pairs of conjunctival appendages: first stout, L-shaped horns, heavily sclerotized; second long, heavily sclerotized, apically flattened, and blade-like.

Vesica simply constructed, seminal duct (fig. 40) opening ventrally into a wide sclerotized tube, posteriorly dilated forming ejaculatory reservoir; anteriorly extended as a wide endophallic duct, latter apically membranous.

*Homaemus aeneifrons* (Say), 1824

Pygophoral opening roughly hexagonal (fig. 41), dorsal margin broad bearing a number of fine setae, laterally dorsal margin bears a small pointed projection on each side. Ventral margin flattened somewhat medianly.

Claspers (fig. 42) hook-shaped, with a stout stem, a number of long setae at base of hook.

Theca (fig. 43) small, conical. Three pairs of conjunctival appendages: first (fig. 44) basally voluminous membranous structures, apically bearing a heavily sclerotized horn; second, small, elongate, membranous structures; third broad and flattened, moderately sclerotized and with numerous small teeth scattered over outer surface (fig. 45).

Base of vesica resembling a nautilus shell (fig. 46), coiled and with a number of pseudopartitions; central portion of coil attached on either side to common base of conjunctival appendages. Apex of vesica broadly rounded, armed with a large number of small spines. Seminal duct extending ventrally into apical half of vesica and into a wide endophallic duct, latter bent through 90°, apically membranous and opening into a membranous pouch on mid dorsal surface of vesica. Ejaculatory reservoir small and continuous with endophallic duct. The coiled structure at the base of the vesica may enable fluids to be pumped into the appendages thereby expanding them. The vesica is very similar to that of *H. aeneifrons consors* examined by Kumar (1965).

*Tetyra antillarum* (Kirkaldy), 1909

Pygophore with dorsal border acutely arched (fig. 47), laterally bearing two smooth sausage-shaped calluses one on each side lying just above apex of claspers. Ventral border sinuous bearing a rounded ridge on ventral surface. Lateral margins with numerous short setae; ventral border with long fine setae.

Claspers (fig. 48) hook-shaped, bifid at apex, outer tooth acute, inner tooth blunt, both heavily sclerotized. Stem short, squat, bearing a number of long setae on a slight promontory at junction with hook.

Theca (fig. 49) small, cone-shaped. Two pairs of fairly large conjunctival appendages first (fig. 50) fused basally for about half their length, apically bearing a small heavily sclerotized point; second also basally fused, apical two-thirds free and capped with a long heavily sclerotized horn.

Vesica, long and narrow, heavily sclerotized; dorsal margin bearing a triangular sclerotized supra vesical process (fig. 51). Seminal duct merging ventrally into a wide S-shaped endophallic duct; ejaculatory reservoir, small crescent-shaped, opening into base of endophallic duct.

*Sphyrocoris obliquus* (Germar), 1839

Pygophoral opening surrounded by a wide flange dorsally and laterally (fig. 52): ventral margin flattened forming a lip with a slight median indentation. Fine setae found on lateral margins and along ventral border.

Claspers (fig. 53) scythe-shaped, stem short and stout; base of hook bearing a number of large stout setae. Inner surface of hook scalloped.

Theca (fig. 54) small, cup-shaped. Two pairs of conjunctival appendages: first membranous broadly rounded at apex and fused to margin of theca; second basally membranous, apically bearing a small heavily sclerotized horn.

Vesica (fig. 55) divided into two parts, ventral portion widely V-shaped, apex blunt bearing a large number of barbs. Dorsally and in apposition is a wide supra-vesical process marked with a number of striae, upper margin with a groove and bearing a number of small sharp teeth; this process fused to base of vesica.

Endophallic duct (fig. 56) opening into a small anterior sinus at the base of the ejaculatory duct, latter fairly straight, situated along ventral arm of vesica opening at its apex. Ejaculatory reservoir pear-shaped, lying above and directly connected to anterior sinus.

*Stethaulax marmoratus* (Say), 1831

Dorsal border of pygophore (fig. 57) diffuse with a small notch just above base of clasper on each side, ventral margin flattened.

Claspers (fig. 58) small club-like structures, apically produced into a small beak-like point, a number of long setae laterally and beneath the apex on the stem, apex minutely scalloped on both sides.

Theca (fig. 59) small, cup-shaped with a shallow median groove on the ventral margin, lateral surfaces with a number of very minute spines scattered in a band just below the margin. Two pairs of conjunctival appendages: first long, cylindrical, basally membranous, apically with a heavily sclerotized bluntly rounded tip; second basally membranous, broad, apically produced into a long heavily sclerotized horn.

Vesica (fig. 60), apex broad, flattened in a dorso-ventral plane. Seminal duct (fig. 61) opening ventrally into a small sinus, lying above and connected to latter is a small elongate dorsal reservoir. Extending back from sinus is a wide duct (figs. 61, 62) becoming convoluted and thickened, posteriorly widening into dorsal chamber of ejaculatory

reservoir, lying beneath is a ventral chamber connected to upper chamber by a narrow passage. Endophallic duct L-shaped originating from entrance of seminal duct.

*Symphylus caribbeanus* (Kirdaldy), 1909

Dorsal margin of pygophore broad (fig. 63), extending laterally and merging into flattened ventral margin. Ventral and lateral margins with numerous long fine setae, proctiger distally also covered with fine setae.

Claspers (fig. 64) heavily sclerotized hammer-shaped, stem centrally swollen, fused at right angles to cross arm one side of which is longer than the other; longer arm bearing two small teeth apically, one on upper margin and one on lower; short arm bearing one tooth on lower margin. Lateral surfaces of head finely scalloped, a number of stout setae on stem below junction with head.

Theca (fig. 65) small, globose. Two pairs of conjunctival appendages: first blade-like moderately sclerotized apically acute; second very long cylindrical membranous, apically bearing a heavily sclerotized horn. Median penal lobes present, dorsally fused together around base of vesica, apically free forming two broad flat plates (fig. 66) on either side of apex of ejaculatory duct; ventral margin with a number of peg-like teeth (fig. 65).

Seminal duct (fig. 67) opening ventrally into a small bilobed anterior sinus; from latter a wide duct opening into dorsal chamber of ejaculatory reservoir. Dorsal chamber connected to a large ventral chamber by means of a narrow passage. Endophallic duct extending from anterior sinus, short and straight, apically terminating a short distance beyond the margins of the median penal lobes.

*Diolcus irroratus* (Fabricius), 1775

Dorsal border of pygophore U-shaped (fig. 68), laterally with two C-shaped indentations lying adjacent to apices of claspers on each side. Ventral border narrow, flattened, slightly sinuate. Fine setae on lateral and ventral margins.

Claspers (fig. 69) with stout stem, apically produced into a short blunt hook. Inner margin of hook scalloped. A few stout setae at base of hook and along outer lateral margin of stem: numerous very small fine spines along the inner lateral margin.

Theca (fig. 70) small, conical, dorsal surface greatly enlarged and produced into two large flat horns one on each side with a wide U-shaped emargination between them. One pair of cylindrical conjunctival appendages, membranous, apically bearing a heavily sclerotized gently curved horn.

Vesica situated in a large oblong membranous conjunctiva, (fig. 71) long narrow and sclerotized; seminal duct (fig. 72) passing straight into ejaculatory duct; no ejaculatory reservoir. A small ventrally projecting apodeme attached at junction of endophallic duct and seminal duct. A deep sclerotized pit borne dorsally within conjunctiva; beneath this pit and immediately above basal half of vesica is a band of muscle fibres. This whole structure may be some type of pumping device.



*Acantholomidea porosa* (Germar), 1839

Pygophore (fig. 73) somewhat oblong in outline, opening surrounded on dorsal and lateral margins by a fairly wide flange, ventral margin narrow centrally. Proctiger heavily sclerotized, antero-dorsally extended into a V-shaped process lying on top of ventral margin of pygophore. A number of minute setae on ventral margin and a number of stout setae on posterior margin of proctiger.

Claspers (fig. 74) with long stem, apically with a shallow hook, a few stout setae situated at base of hook.

Theca (fig. 75) small squat broader than long. Three pairs of conjunctival appendages (fig. 76): first large horn-like structures, sclerotized almost to base which is membranous; second smaller, membranous squat structures, bearing apically a pair of stout heavily sclerotized curved spines; third narrow cylindrical, sclerotized structures, apically acute.

Seminal duct (fig. 78) entering into a wide endophallic duct latter extremely short, not extending past margin of ejaculatory reservoir. From endophallic duct posteriorly is a wide duct opening into an S-shaped ejaculatory reservoir; latter divided by a septum into a large dorsal chamber and a smaller ventral chamber.

*Scutellerini**Augocoris gomesii* (Burmeister), 1835

Pygophore with dorsal border (fig. 79) smoothly rounded; ventral border with two deep V-shaped emarginations on either side of a stout blunt median process, lateral margins produced into blunt points. Dorsal and ventral margins covered with long fine setae.

Theca heavily sclerotized, cylindrical with two small protuberances on antero-dorsal margin (fig. 81) one on each side of mid-line. Two pairs of conjunctival appendages: first (fig. 82) bifid, one branch completely membranous, cylindrical, blunt at apex, the other sclerotized, broadly rounded at apex, common base membranous; a sclerotized band round base of first conjunctival appendages, probably represents remains of second (Leston 1952); third typically scutellerine, heavily sclerotized, cylindrical, and apically acute.

Seminal duct (fig. 83) connected directly into base of endophallic duct; a long convoluted duct leading back from entrance of seminal duct, expanding dorsally into an elongate ejaculatory reservoir, latter connected by a canal to a large dorsal sinus; a short stout endophallic duct attached apically to sinus.

**Pentatomidae - Pentatominae***Pentatomini**Pentatoma rufipes* (Linnaeus), 1758

Described and figured by Piotrowski (1950). However, because his description is in Polish a second description in English is not out of



place.

Dorsal border of pygophore (fig. 84) broadly arched medianly with a small bilobed superior ridge. Ventral border deeply concave (fig. 85) centrally with a narrow U-shaped inferior ridge, internally forming two ridges (superior rests of Leston 1954).

Claspers (fig. 86) C-shaped and strap-like; divided into two arms, upper arm apically divided into a proximal broadly rounded lobe and a distal elongate process, lower arm fused to margin of pygophore, apically heavily sclerotized and produced into a broad flattened flange.

Theca (fig. 87) long, cylindrical. One pair of conjunctival appendages; cylindrical very lightly sclerotized; apically produced into two blunt lobes. Median penal lobes (fig. 88) fused to form a cone around apex of vesica with lateral margins somewhat thickened and produced into blunt points dorsally.

Seminal duct (fig. 89) merging apically into a canal found along ventral and dorsal margins of box-like ejaculatory reservoir; reservoir with an oval anterior chamber (fig. 89) separated by an incomplete septum; canal opening into this chamber dorsally. Base of endophallic duct inserted into reservoir ventrally; duct short, slightly kinked, apically terminating between median penal lobes.

*Dendrocoris humeralis* (Uhler), 1877

Dorsal border of pygophore (fig. 90) with a narrow superior ridge; lying one on either side is a pair of oblong genital plates (fig. 91) upper surfaces finely scalloped. Ventral border produced into two large triangular platforms one on each side with a deep median trough between them, outer margin of trough with a deep median U-shaped emargination (fig. 92).

Claspers (fig. 93) flattened, broad, apex emarginate, heavily sclerotized, dorsal margin apically terminating in a point, ventro-apical margin broadly rounded. Clasper somewhat C-shaped in outline inner apical margin finely scalloped.

Theca elongate, cylindrical. One pair of conjunctival appendages (fig. 94), membranous baggy structures, apically broadly rounded (not fully inflated in fig.), an elongate cylindrical dorsal conjunctival lobe present and a second broadly rounded balloon-like lobe found ventrally (fig. 95), enclosed by conjunctival appendages, probably representing greatly modified median penal lobes.

Ejaculatory reservoir large, divided by means of septae into a series of ducts. Seminal duct (fig. 95) merging ventrally into a long canal leading round base of reservoir to apico-dorsal region and into a duct which in turn opens into a central sinus. Base of endophallic duct continuous with central sinus, duct wide, U-shaped, bearing a small flange ventro-basally.

*Piezodorus lituratus* (Fabricius), 1794

Claspers, aedoeagus and vesica figured by Pruthi (1925).

Pygophore with dorsal border (fig. 96) widely U-shaped, opening of pygophore small. Ventral border with a shallow median emargination, gently sloping dorsad on either side. Ventral surface beneath border

almost vertical with two shallow median depressions. A number of stout setae found along margins.

Claspers (fig. 97) with fairly broad stem apically bent at right angles forming a short triangular head, outer lateral margin finely scalloped.

Theca small, oval in outline. Two pairs of conjunctival appendages (fig. 98): first membranous, cylindrical, apically tapering slightly to a sclerotized blunt apex, basally produced into four conjunctival lobes; second basally membranous, cylindrical, apically bearing a heavily sclerotized horn. Median penal lobes (fig. 99) flattened and leaf-like, fused along their dorsal margins, and to the sub-apical portion of the vesica.

Ejaculatory reservoir (fig. 100) divided into two chambers by means of a stout sclerotized septum. Seminal duct merging ventrally into a narrow canal passing round posterior margin of ejaculatory reservoir to open into anterior chamber. Endophallic duct opening out from posterior chamber of ejaculatory reservoir, moderately long and sinuous, apically terminating between median penal lobes.

*Solubea pugnax* (Fabricius), 1775

Pygophore (fig. 101) and claspers (fig. 102) described by Sailer (1944).

Theca (fig. 103) cylindrical with a short membranous hinge attaching it to basal plates. One pair of conjunctival appendages, small, moderately sclerotized throughout, apically broadly rounded. Median penal lobes forming a cylindrical sheath round apex of vesica (fig. 104), apical lateral margins heavily sclerotized forming a flat plate ventrally on each side, dorsally lobes fused together by means of a membrane.

Seminal duct (fig. 105) enclosed in a thick membranous sheath, opening ventrally into base of endophallic duct; latter moderately long enclosed in a stout cylindrical sheath, apically bent through  $90^{\circ}$ , basally widening into a small bulb-like ejaculatory reservoir.

*Peribalus limbolarius* (Stål), 1872

Pygophore (fig. 106) and claspers (fig. 107) described by Baker (1931).

Theca (fig. 108) vasiform expanded anteriorly into a large thecal shield; two pairs of processes on each side of theca; anterior processes smaller, heavily sclerotized, broadly rounded apically; posterior processes smaller, heavily sclerotized, broadly rounded. One pair of membranous conjunctival appendages divided into two broad lobes. Median penal lobes (fig. 109) flattened laterally into two wide sclerotized plates, ventro-apical margins finely serrate, basally united by a narrow cross-bar one third distance from their bases, lobes not enclosing apex of vesica.

Ejaculatory reservoir (fig. 110) somewhat oblong with a canal round posterior surface into which seminal duct enters ventrally. Endophallic duct narrow, sinuous, basally opening into apex of reservoir.

*Trichopepla semivittata* (Say), 1832

Pygophore with dorsal border (fig. 111) deeply and evenly arched, bearing a small protuberance on each side; ventral border (fig. 112) widely U-shaped. Two flat leaf-like genital plates one on either side lying beneath the protuberance on the dorsal border.

Claspers (fig. 113) C-shaped, bifid at apex, no differentiation between stem and apex; five fine setae on inner margin.

Theca lightly sclerotized, cylindrical and tapering apically. One pair of conjunctival appendages (fig. 114), membraneous except for a line of sclerotization along ventral margin, apically broadly rounded. Median penal lobes absent.

Seminal duct ventrally opening into a simple globular ejaculatory reservoir. Endophallic duct heavily sclerotized, attached to reservoir dorsally, duct long, thin and sinuous, apically a fine needle-like point.

*Mormidea lugens* (Fabricius), 1775

Pygophoral opening small (fig. 115), surrounded by wide margins, dorsal border deeply arched; ventral border medianly U-shaped with two acute prominences one on either side of emargination.

Claspers (fig. 116) very small, stout oblong structures, apically very broadly rounded.

Theca (fig. 117) small, squat. One pair of membraneous balloon-like conjunctival appendages. A large sheath-like structure present, probably fused median penal lobes; moderately sclerotized, ventrally with a deep cleft, basally narrowed and forming a short cylindrical stem; whole structure surrounding apex of vesica.

Endophallic duct (fig. 118) moderately long bearing two sclerotized flanges, medianly wide, rounded, apically tapering, basally endophallic duct expanding into a small bulb-like ejaculatory reservoir. Seminal duct connecting with base of ejaculatory duct ventrally.

*Brepholoxa heidemanni* (Van Duzee), 1904

Opening of pygophore dorsad (fig. 119) and somewhat triangular. Dorsal border shallowly concave with a narrow superior ridge not clearly differentiated from border proper. Ventral border with two elongate calluses forming a V; a deep U-shaped notch formed between apices of calluses. Two further notches found, one on either side between junction of dorsal and ventral borders.

Claspers (figs. 120, 121) with short, stout stem, C-shaped, bearing apically a small heavily sclerotized triangular pad, finely scalloped, a second triangular pad found below apical one also finely scalloped.

Theca small, cylindrical. One pair of conjunctival appendages (fig. 122) divided into three broad membraneous lobes, ventral most fused together forming a platform beneath apex of vesica; dorsal lobes largest, somewhat leaf-like.

Ejaculatory reservoir (fig. 123) membraneous, oval, with a pair of septa attached to dorsal surface, reaching mid way into reservoir forming an upper chamber. A canal leads from apico-ventral surface round posterior margin of reservoir to open apically into an upper chamber. Seminal duct inserted directly into this canal. Endophallic duct



originating from apex of lower chamber of reservoir, short and curved through 90°.

*Arvelius albopunctatus* (DeGeer), 1773

Dorsal border of pygophore deeply concave (fig. 124) with two rounded projections laterally, (fig. 125) one on each side; ventral border also deeply concave, margin flattened into a lip bearing two longitudinal ridges.

Claspers (fig. 126) F-shaped, distal arm apically bluntly bilobed.

Theca cylindrical with two small sharply pointed processes on dorsal margin (fig. 127). One pair of conjunctival appendages composed of three membranous rounded lobes fused onto a common base and a dorsal median conjunctival lobe. Median penial lobes consisting of a flat pair of plates apically truncate, lobes fused along their lower margins forming a trough around apex of vesica.

Seminal duct (fig. 128) opening medianly into a wide canal round base of ejaculatory reservoir and connected to a dorso-apical chamber; ejaculatory reservoir oval incompletely divided by means of a stout septum into two chambers. Endophallic duct S-shaped basally, originating from apico-ventral half of ejaculatory reservoir.

*Aelia americana* (Dallas), 1854

Pygophore (fig. 129) and claspers (fig. 130) described by Baker (1931).

Theca (fig. 131) cylindrical somewhat diamond-shaped in dorso-ventral plane due to two lateral conical projections, one on each side; dorsal margin produced into a thecal shield. One pair of conjunctival appendages, broad, membranous lobes rounded apically; when fully inflated balloon-like. A large membranous conjunctival lobe present. Median penial lobes (fig. 132) small, thin, heavily sclerotized, fused to a wide common base.

Seminal duct (fig. 133) inserted directly into a long canal which opens by means of a valve-like arrangement into dorso-apical region of ejaculatory reservoir, latter lying centrally, apically merging into a sinuous endophallic duct with spout-like apex.

*Vulsirea violacea* (Fabricius), 1803

Pygophore with dorsal margin (fig. 134) bearing two oval patches of short heavily sclerotized setae one on either side, similar to patches of setae found in Scutellerinae (McDonald 1961), however in this species setae not arranged in rows. Ventral margin gently concave bearing laterally on each side a stout finger-like process, further behind these is a pair of stout bifid processes one on each side; a narrow ridged floor with a deep median V-shaped cleft running between these inner pygophoral processes.

Claspers (fig. 135) with stem short, apically produced into three lobes. Outer surfaces of lobes finely scalloped.

Theca small, somewhat oblong (fig. 136). Two pairs of conjunctival appendages: first membranous, basally wide, apically produced into a narrow sclerotized point; second membranous, cylindrical,



apically blunt, basally fused to the first. Median penal lobes (fig. 137) disc-like, medianly fused to one another and to sub-apex of vesica, basally each lobe produced into a bifid process.

Ejaculatory reservoir (fig. 138) large with a partial septum dividing it into two chambers. Seminal duct inserted into base of endophallic duct, from this point is a long duct slightly convoluted posteriorly opening into the apico-dorsal portion of ejaculatory reservoir. Endophallic duct wide and short, fused between median penal lobes.

*Acrosternum pennsylvanicum* (DeGeer), 1773

Dorsal border of pygophore with a broad superior ridge (fig. 139). Ventral border shallowly concave (fig. 140), two flat processes found on margin one on either side, outer margin concave with a number of very heavily sclerotized teeth.

Claspers (fig. 141) simple, spear-shaped with a very short stout stem.

Theca small, cylindrical. One pair of small membraneous conjunctival appendages (fig. 142) attached to a large membraneous base. Median penal lobes tubular, sclerotized, with a small expanded head apically, basally fused to a common stem.

Seminal duct (fig. 143) opening ventrally into a simple sac-like and membraneous ejaculatory reservoir. Endophallic duct passing forward from apex of reservoir, slightly kinked, short, apically terminating between apices of median penal lobes.

*Chlorocoris subrugosus* (Stal), 1872

Pygophore with dorsal border (fig. 144) medianly evenly arched, laterally bearing two small projections one on each side; ventral border (fig. 145) deeply concave, sinuate, medianly with a bilobed inferior ridge with a minute spine on either side laterally. Proctiger long, narrow, bearing apically two flat lobes covered with a mat of fine setae.

Apex of claspers formed into a trilobed umbrella-like structure (fig. 146) stem short and slender, upper surface of apex covered with a dense mat of fine setae.

Theca large, cylindrical with very large basal plates; apically produced into a short cylindrical thecal shield (fig. 147) surrounding the sub-apical portion of the vesica. No conjunctival appendages or median penal lobes.

Seminal duct wide passing medianly into a canal, latter encircles posterior end of ejaculatory reservoir and opens dorsally. Ejaculatory reservoir simple sac-like, endophallic duct originating from posterior end of reservoir as a wide duct, narrowing anteriorly, short, slightly curved, apically terminating a short distance beyond thecal shield.

*Carpocoris remotus* (Horvath), 1907

Pygophoral opening wide, triangular (fig. 148); dorsal border widely arched bearing two large cone-shaped lateral projections one on either side of mid line; lying beneath these, one on each side, thin saucer-like genital plates (fig. 149), very lightly sclerotized with a fringed margin and numerous small spines on upper surface. Ventral

border (fig. 150) with a small median V-shaped emargination and two rounded prominences one on either side of median emargination.

Claspers (fig. 151) with short stout stem produced into a flattened oblong leaf-like apex bearing a sharp tooth on lower angle, dorsal surface deeply cleft.

Theca (fig. 152) small, squat with two small projections one each side, on the apical margin in a dorso-lateral position. One pair of membranous conjunctival appendages (figs. 152, 153), leaf-like, with a sharp sclerotized ridge along ventral margin.

Ejaculatory reservoir (fig. 154) sac-like with posterior canal into which seminal duct opens ventrally. Endophallic duct long S-shaped, basally entering apex of reservoir, apex spout-like.

*Nezara viridula* (Linnaeus), 1758

Described and figured by Pruthi (1925). Additional descriptions and corrections given below.

Pygophore, dorsal border concave with a very narrow superior ridge (fig. 155); ventral border (fig. 156) with a deep emargination.

Claspers (fig. 157) with inner surface finely scalloped.

Theca moderately long, cylindrical. One pair of small membranous conjunctival appendages (fig. 158), very short, broad (apparently not noted by Pruthi). Median penial lobes (fig. 159) semi-circular, fused together into a broad U along ventral margins, enclosing apex of vesica.

Vesica described and figured by Kumar (1964). Seminal duct (fig. 160) merging into a wide funnel-shaped canal (conducting canal of Kumar), canal narrowing, encircling posterior margin of ejaculatory reservoir and opening dorsally. Ejaculatory reservoir oval; endophallic duct short and slightly sinuous, basally merging with apex of reservoir.

*Thyanta perditor* (Fabricius), 1794

Pygophore somewhat globular, pygophoral opening small, facing caudad; dorsal margin with a very narrow superior ridge (fig. 161). Ventral border with a deep median V-shaped notch. Stout setae on lateral margins.

Claspers C-shaped (fig. 162), upper margin straight, bearing a number of fine setae, basal margin broad, stout, forming stem.

Theca balloon-like and acentric, two small knobs (fig. 163) one on each side on dorsal surface near apex. One pair of conjunctival appendages, dorsally produced into an oblong membranous process, basally appendage wide, apically tapering into a sclerotized horn. Median penial lobes (fig. 164) cylindrical and curved in a U on either side of apex of vesica, each with a pointed tooth apically, heavily sclerotized throughout.

Vesica very similar in construction to *Chlorocoris subrugosus*, ejaculatory reservoir (fig. 165) very large, globular, endophallic duct narrow and short.

*Padaeus viduus* (Vollenhoven), 1868

Dorsal border of pygophore with a narrow superior ridge (fig.

166); ventral margin flattened, border with a median V-shaped notch, two ridges, one on each side, forming a wide V, run from outer angles of ventral margin to centre of pygophore.

Claspers (fig. 167) flattened, basally wide, apically produced into a blunt point, a line of fine scalloping running from apex a short distance down inner surface.

Theca (fig. 168) oval in shape. Two pairs of conjunctival appendages (fig. 169): first heavily sclerotized, rod-like; second bifid; dorsal arm membraneous balloon-like; ventral arm apically sclerotized and oblong in outline. Median penal lobes (fig. 170) fused into a horseshoe-like shield surrounding apex of vesica (fig. 171).

Vesica consisting internally of a complicated series of ducts. Seminal duct (fig. 172) passing ventrally into a long canal opening into dorsal half of ejaculatory reservoir; latter divided into dorsal and ventral ducts. Endophallic duct short, basally widening and merging into ventral chamber.

*Proxys punctulatus* (Palisot de Beauvois), 1805

Dorsal border of pygophore medianly with a well developed superior ridge (fig. 173), laterally bearing a small oblong projection on each side. Ventral margin flattened, border with a wide median U-shaped emargination, on either side of which is an oblong callus (fig. 174) bearing a number of setae; running back from each callus is a pair of well sclerotized ridges medianly forming between them a U-shaped trough.

Claspers (fig. 175) with stout wide stem, produced apically into a blunt cylindrical process, inner margin with a narrow band of scalloping. Five or six small stout setae found on margin of stem.

Aedoeagus and vesica similar in most respects to those of *Padaeus viduus*. Second conjunctival appendages (fig. 176) somewhat more sclerotized than in *P. viduus*. The general similarity of the genitalia of this species to that of *P. viduus* would suggest that these 2 genera are closely related and that *Padaeus* should be placed in *Proxys*.

*Neottiglossa trilineata* (Kirby), 1837

Pygophore with dorsal border (fig. 177) evenly arched, laterally bearing on each side a rounded lobe with a fringe of hairs. Ventral border almost straight with a wide median emargination, ventral margin below border almost vertical.

Claspers (fig. 178) with stout oblong stem apically produced on inner side into a flat plate and on outer side into a short blunt process.

Theca short, stout, bearing laterally two large knobs (fig. 179) one on either side; apex of theca produced dorsally into a thecal shield consisting of two pointed lobes with a wide U-shaped depression between them. One pair of membraneous conjunctival appendages, apically broadly rounded; dorsal to these is a large and voluminous conjunctival lobe (not fully expanded in fig.). Median penal lobes sclerotized, cylindrical, and curved inwards, fused basally along their ventral margins and connected to sub-apex of vesica by two thickened arms one on each side.

Seminal duct (fig. 180) opening ventrally into a wide canal extending round base of reservoir and opening into a simple sac-like ejaculatory reservoir. Endophallic duct short, slightly sinuous, entering ejaculatory reservoir apically.

*Murgantia histrionica* (Hahn), 1834

Pygophore with dorsal border (fig. 181) deeply arched and somewhat  $\Omega$  shaped; ventral border sinuous with a wide median U-shaped concavity, two small processes borne one on either side of the ventral border on the lateral margins. Proctiger box-like, centrally concave and produced into two flattened median processes distally.

Claspers (fig. 182) flattened basally, apically narrowing into blunt curved rods, no differentiation between stem and apex.

Theca oblong, bearing distally a large cylindrical thecal shield (fig. 183). One pair of long cylindrical, membraneous conjunctival appendages (not fully expanded in fig.), apically blunt and moderately sclerotized. Median penal lobes hook-like, basally fused to a common stem dorso-medianly, apices connected by a small plate bearing a conical cap (fig. 184) fitting over apex of vesica.

Ejaculatory reservoir (fig. 185) S-shaped, terminating in a closed chamber. Seminal duct opening ventrally into base of endophallic duct, latter proximally connected to apical chamber of ejaculatory reservoir, distally narrowing into a slightly curved duct, apically attached to median penal lobes.

*Eysarcoris aeneus* (Scopoli), 1763

Pygophore with dorsal border (fig. 186) sinuous; ventral border with a deep median U-shaped emargination, on each side of which is triangular flattened area bearing a number of setae. Proctiger apically with a median bilobed sclerotized process.

Claspers divided into two sections (figs. 187, 188), a broad flattened diamond shaped blade apically acute and a semi-circular platform attached to base of blade, a number of setae around margin; outer edge finely scalloped.

Theca (fig. 189) conical, flattened laterally. Two pairs of conjunctival appendages: first (fig. 190) membraneous, elongate, tube-like, fused together basally, apically bluntly rounded; second bifid, consisting of two heavily sclerotized, flattened, spatula-like appendages, fused basally and tapering into a long pointed process.

Ejaculatory reservoir (fig. 191) small globose with a canal round posterior margin into which seminal duct opens ventro-apically. Endophallic duct long, sinuous, connected basally to apex of ejaculatory reservoir.

*Eysarcoris intergressus* (Uhler), 1893

Pygophore with dorsal border (fig. 192) evenly arched bearing on either side of the mid-line a small triangular genital plate; ventral border with an inferior ridge, centrally below the ventral border is a shallow depression.

Claspers chisel-like (fig. 193) bilobed apically, a number of



stout setae on outer surface.

Theca tubular (fig. 194). One pair of conjunctival appendages (fig. 195) divided into two arms, a large ventral cylindrical membranous appendage, apically tapering to a sclerotized point; at base of this large arm is a small dorsal cylindrical appendage, apically blunt. A pair of rounded slightly sclerotized ventral conjunctival lobes present, fused to common base of conjunctival appendages.

Vesica very similar to *Cosmopepla bimaculata*, endophallic duct more loosely S-shaped (fig. 196).

*Eysarcoris intergressus* shows no similarity with the European species *E. aeneus* studied but shows very great similarity to *Cosmopepla* in possessing genital plates, chisel-like claspers and a very similar aedoeagus and vesica. It is suggested that *Eysarcoris* should be placed in *Cosmopepla*. The European species *Eysarcoris aeneus* possess no genital plates, very peculiar claspers and the shape of the conjunctival appendages is quite different; the vesica shows some similarity.

*Cosmopepla bimaculata* (Thomas), 1865

Pygophore (fig. 197) and claspers (fig. 198) described by Baker (1931).

Theca cylindrical, somewhat curved when viewed laterally, two small projections (fig. 199) one on each side near base of theca. One pair of conjunctival appendages each divided into a large membranous cylindrical lobe, apically tapering to a blunt sclerotized point, and a second small rounded sclerotized lobe, borne dorsally. A pair of small rounded conjunctival lobes ventral to conjunctival appendages may represent second conjunctival appendages. No median penial lobes.

Seminal duct (fig. 200) opening ventrally into a narrow canal encircling posterior end of reservoir, and terminating dorsally. Endophallic duct long, broadly S-shaped entering ejaculatory reservoir through a groove formed by two sclerotized ridges on apex of reservoir.

*Rhytidolomia senilis* (Say), 1831

*Rhytidolomia viridicata* (Walker), 1867

*Rhytidolomia saucia* (Say), 1831

*Chlorochroa sayi* (Stål), 1872

*Chlorochroa ligata* (Say), 1831

*Chlorochroa uhleri* (Stål), 1872

From a study of the male genitalia alone it is very clear that these species are all very closely related to one another and should all be included in the genus *Rhytidolomia*. This fact was suspected by Sailer (1954) who also found that three of the species of *Chlorochroa* broke down into a maze of intermediate populations. A thorough study is needed to elucidate the validity of species included within the genus *Rhytidolomia*.

*Rhytidolomia senilis*

Dorsal border of pygophore with a broad median superior ridge (fig. 201) passing down on each side round the base of the proctiger. Ventral border gently concave with a trilobed inferior ridge. Ventral and dorsal margins covered with fine setae.

Claspers (fig. 202) with a stout stem apically produced into three

blunt lobes. A number of fine setae on outer and inner apical surfaces.

Theca cylindrical, flattened slightly laterally. One pair of membraneous conjunctival appendages (fig. 203), basally broad, apically broadly bilobed, a long membraneous blunt dorsal lobe at the base of which is a ventral lobe with heavily sclerotized apical point. Median penal lobes (fig. 204) club-like, basally fused along their dorsal margins.

Seminal duct (fig. 205), opening ventrally into a heavily sclerotized canal, latter widening posteriorly and opening mid-dorsally into an oval ejaculatory reservoir. Endophallic duct short, almost straight, merging into apex of reservoir.

*Rhytidolomia viridicata*

Pygophore (fig. 206) and claspers (figs. 207, 208), very similar to *R. senilis*, lobes of clasper somewhat more rounded.

Aedoeagus and vesica - similar to *R. senilis*, conjunctival appendages divided into two completely membraneous lobes, no sclerotized apical point present.

*Rhytidolomia saucia*

Pygophore (fig. 211) and claspers (fig. 212) similar to *R. senilis*, shape of lobes at apex of claspers differs slightly, outer lobe acute.

Aedoeagus (fig. 213) and vesica (fig. 214) similar in most respects to those of *R. senilis*. However differences exist in the basal plates of the theca, useable at a specific level.

*Chlorochroa ligata*

Dorsal border of pygophore with superior ridge (fig. 215) extending laterally on each side in an arc forming a small lateral projection. Ventral border sinuous with a shallow median emargination.

Claspers apically trilobed (fig. 216) very similar to *C. uhleri*, slight differences in shape exist, however.

Aedoeagus and vesica, similar to those of *Rhytidolomia senilis*.

*Chlorochroa uhleri*      *Chlorochroa sayi*

Pygophore (fig. 217), claspers (figs. 218, 219) and aedoeagus described by Baker (1934). The genitalia of these species are similar in all respects. Aedoeagus and vesica similar to *Rhytidolomia senilis*.

*Banasa dimidiata* (Say), 1831

Dorsal border of pygophore with a wide superior ridge (fig. 220) with a median emargination. Ventral border flattened bearing two double knobbed processes one on each side of a median square projection on the border. Proctiger and margins of pygophore covered with fine setae.

Claspers (fig. 221) flattened, leaf-like, covered with fine setae.

Theca oblong, compressed laterally. One pair of membraneous conjunctival appendages (fig. 222), broadly rounded apically. Median penal lobes elongate, spatulate, apically free, broadly rounded, medianly fused on the ventral surface, not enclosing apex of vesica.

Ejaculatory reservoir (fig. 223) oval, simple; seminal duct opening into reservoir antero-ventrally; a canal extending from entrance

of ductus seminis around posterior portion of reservoir to open anterodorsally. Endophallic duct short, slightly curved basally, connected to apex of ejaculatory reservoir, apex of duct enclosed in a broad sclerotized sheath.

*Loxa flavicollis* (Drury), 1773

Pygophore with dorsal border (fig. 224) evenly arched, ventral border deeply concave and flattened. An unusual pair of pygophoral appendages (fig. 225) borne medianly, one on each side at the base of dorsal margin; apex triangular in shape, with a broad concave surface, produced into a long arm basally truncate, apex with long stout setae.

Claspers unusual (fig. 226), stem short, apex broad bearing seven processes on outer margin, six blunt and oblong, apical process produced into an acute point. Fine setae found over surface. Clasper resembles a drilling bit when viewed apically.

Theca (fig. 277) small, acentric, with very large and well developed basal plates; basal half of theca oblong becoming constricted medianly and curving dorsad and produced into a semi-circular plate, latter bearing a large bowl-like structure (thecal shield) with crenulated margins (fig. 228). From centre of thecal sheath a second sheath, probably fused median penal lobes, surrounds apex of vesica. No conjunctival appendages present.

Seminal duct (fig. 229) inserted ventrally into a heavily sclerotized canal, latter passing round base of ejaculatory reservoir and terminating apically in a small 180° turn capped by a large sclerotized apodeme. Ejaculatory reservoir very small, endophallic duct basally continuous with reservoir.

*Loxa flavicollis* presents a most aberrant type of genitalia. It is unique amongst specimens examined in possessing the unusual median penal lobes, no conjunctival appendages, and the peculiar sheath developed on the margin of the theca. The vesica is also extremely simple and possesses an unusual pumping mechanism. On the basis of these distinct peculiarities *Loxa* could be placed in a sub-tribe of its own, however this would probably be better left till further work has been done on other species of *Loxa*.

*Menecles insertus* (Say), 1831

Pygophore (figs. 230, 231) and claspers (fig. 232) described by Baker (1931).

Theca vasiform with a pair of finger-like thecal processes (fig. 234). Two conjunctival appendages present, both membraneous and fused to a wide common base: first (fig. 233) long thin cylindrical structures, apically blunt; second short, broad, bearing five small lobes. Median penal lobes (fig. 235) flattened and fused together forming a deep narrow groove between lobes in which apex of vesica is situated.

Seminal duct (fig. 236) connected ventrally to wide base of endophallic duct, latter merging posteriorly into a broad very heavily sclerotized ejaculatory reservoir with heavy striae on its lateral margins. Endophallic duct anteriorly narrow, very long and coiled around itself in a series of loops on right side of theca.



*Coenus delius* (Say), 1831

Pygophore (fig. 237) and claspers (fig. 238) described by Baker (1931).

Aedeagus figured and described by Baker (1931), his lateral penal lobes (= conjunctival appendages) were not fully expanded. Theca vasiform with an apical overhanging rim, a pair of elongate finger-like thecal processes (fig. 239) on dorsal margin of theca (titillators of Baker). One pair of conjunctival appendages (fig. 239), membranous, apically tapering and divided into two small blunt processes, one shorter than the other. Median penal lobes (fig. 240) fused into a semi-circular disc-like structure with a wide median groove, apex of vesica lying within this groove.

Seminal duct (fig. 240) heavily sclerotized opening into a small ventral sinus; latter merges posteriorly into a heavily sclerotized oblong ejaculatory reservoir, lateral margins scored with a number of striae running in a ventro-dorsal direction. Endophallic duct basally united to anterior sinus, as a fairly wide duct, then narrowing and looping to right hand side of theca, passing through a wide circle to terminate within apex of median penal lobes.

*Hymenarcys nervosa* (Say), 1832

Pygophore (fig. 241) and claspers (fig. 242) described by Baker (1931).

Theca oblong bearing dorsally a pair of long cylindrical thecal processes (fig. 244). One pair of conjunctival appendages (fig. 243), membranous, very broad and voluminous, apically terminating in a short blunt point. Median penal lobes fused into a semi-circular flange bearing a deep median groove.

Seminal duct (fig. 245) heavily sclerotized, connecting ventrally into wide base of ejaculatory duct which posteriorly communicates with dorsal ejaculatory reservoir. Latter flattened dorso-ventrally, trilobed dorsally and heavily sclerotized, lateral margins with a number of well marked striae. Anteriorly endophallic duct narrows, twists sharply twice passing to right side of theca, then looping in a large circle terminates within groove between median penal lobes.

*Euschistus tristigmus* (Say), 1831

Pygophore (fig. 246) and claspers (fig. 247) described by Baker (1931). Lower apical margin of clasper finely striated.

Aedeagus described by Baker (1931). Theca oblong, with two rounded processes (fig. 249) (titillators, Baker, 1931) dorsally, one on each side of the median line. Two pairs of conjunctival appendages (lateral penal lobes of Baker) fused onto a common membranous base: first (fig. 248) membranous, wide basally, apically acute, slightly sclerotized; second small, apically acute slightly sclerotized, possibly only one bifid appendage represented since these appendages are not sharply divided from one another. Median penal lobes (fig. 249) present, fused into a flat semi-circular plate with a median dorsal groove.

Seminal duct (fig. 250) stout, opening ventrally into ejaculatory reservoir where it is bent through 180°, passing along proximal end of



reservoir to open into a dorsal chamber, latter connecting with a narrow ventral chamber by means of a longitudinal slit-like aperture in septum between dorsal and ventral chambers. Endophallic duct extremely long arising from middle of ventral chamber in ejaculatory reservoir, extending forwards as a wide tube, bending through  $90^{\circ}$  and becoming enclosed by bases of median penal lobes for a short distance; then turning through  $90^{\circ}$  to pass a short distance ventrally and loop round to right hand side of theca, from here looping in an S to finally pass in a wide circle terminating apically on dorsal groove formed by median penal lobes.

*Prionosoma podopioides* (Uhler), 1863

Pygophore with dorsal border (fig. 251) rounded with a broad superior ridge medianly extending down on each side of base of proctiger. Ventral border laterally diffuse, medianly with a U-shaped groove on either side of which is a slightly raised and rounded platform. A number of long fine setae found along dorsal and ventral margins.

Claspers (fig. 252) stout, hook-shaped, stem wide, a number of fine setae on inner margin of hook.

Theca small, oblong, dorsal margin with two long cylindrical thecal processes (fig. 254). One pair of conjunctival appendages (fig. 253), basally wide membraneous, apically divided into two blunt lobes, ventralmost one apically sclerotized. Median penal lobes narrow semi-circular plates fused medianly forming a groove in which apex of vesica rests.

Seminal duct (fig. 256) opening ventrally into a sclerotized canal encircling proximal end of ejaculatory reservoir, latter large, flattened dorso-ventrally, heavily sclerotized and with a number of striae along posterior half. Reservoir with a narrow more membraneous ventral portion forming a duct merging postero-ventrally into wide base of endophallic duct (fig. 255); latter narrowing, looping round in three small turns and finally coiling in a wide circle to apically terminate between median penal lobes.

*Halyini*

*Brochymena arborea* (Say), 1825

Pygophore with dorsal border evenly arched (fig. 257), a wide lateral flange found on either side bearing a patch of thick stout setae; ventral margin concave with a deep median U-shaped emargination.

Claspers described and figured by Ruckes (1946). T-shaped (fig. 258) in outline, stem stout flattened laterally, apically somewhat abruptly narrowed and bearing a cross-arm, situated in a dorso-ventral plane when clasper at rest in pygophore; dorsal arm of T produced into a stout hook, ventral arm blunt and shallowly bilobed apically. Base of stem bearing a small cylindrical process bearing a number of long stout setae.

Theca cylindrical, elongate (fig. 259). One pair of broad membraneous conjunctival appendages, apically produced into a blunt sclerotized point; a narrow band of sclerotization running from apex down inner margin of appendages. Median penal lobes thin rod-like (fig. 260) basally fused to a common stem not enclosing apex of vesica.

Seminal duct (fig. 260) inserted ventro-apically into a long canal encircling posterior margin of ejaculatory reservoir and opening dorso-apically into reservoir; latter large sac-like with a sclerotized apical cap. Endophallic duct basally opening into apex of reservoir, long S-shaped, apically free.

*Brochymena quadripustulata* (Fabricius), 1775

Pygophore figured by Crampton (1922). Dorsal border (fig. 262) widely arched bearing medianly a narrow superior ridge; ventral border (fig. 263) with a median V-shaped emargination in which the apex of the pygophore rests. Numerous long fine setae along dorsal and ventral margins.

Claspers G-shaped (fig. 264), stem stout, produced into a curved hook, a number of long setae at base of hook.

Theca large cylindrical (fig. 265). One pair of conjunctival appendages, small membranous on outer surface, slightly sclerotized on inner surface, apically acutely pointed. Median penal lobes (fig. 266) flattened oblong plates, basally fused to a common base not closely associated with apex of vesica.

Vesica very similar to that of *Brochymena arborea*, shorter (fig. 267).

*Edessini*

*Edessa bifida* (Say), 1832

Pygophore with dorsal border widely arched (fig. 268); ventral border gently concave. A pair of heavily sclerotized peg-like genital plates present, one on each side laterally on dorsal border (fig. 269).

Claspers (fig. 270) with a broad stem merging into a triangular spear-like head set at 45°, inner margin finely scalloped.

Theca (fig. 271) heavily sclerotized elongate and cylindrical. One pair of very small sclerotized conjunctival appendages, broadly hook shaped and fused to margin of theca.

Ejaculatory duct (fig. 272) consisting of a complicated series of parallel ducts, their actual connections could not be worked out adequately in whole mounts even with Kumar's (1964) technique of introducing air into these canals. Seminal duct entering vesica apically. Endophallic duct short, curved. Sections will have to be made to work out the detailed connections of the seminal duct and canals within the ejaculatory reservoir.

*Discocephalini*

*Lineostethus clypeatus* (Stål)<sup>o</sup>, 1862

Dorsal margin of pygophore (fig. 273, 274) with two large rectangular flaps one on either side of a median V-shaped depression. Ventral border (fig. 275) sinuous produced on either side into two narrow downwardly projecting flanges, apically acute and separated by a small U-shaped emargination. Ventral surface below margin with a deep U-shaped depression, a row of small stout setae found along proximal margin.

Claspers (figs. 276, 277) with a narrow stem, cylindrical, apically expanded into a flat triangular plate terminating in a small heavily sclerotized spine; upper surface of blade finely scalloped.

Theca (fig. 278) pyriform with a small rim round apex. No conjunctival appendages. Median penal lobes fused into an oblong envelope-like structure enclosing basal two thirds of the endophallic duct.

Seminal duct (fig. 278) opening into a long canal extending round base of ejaculatory reservoir and opening dorsally. Reservoir flask-shaped, apically merging into endophallic duct; latter with a heavily sclerotized collar at base; apex of endophallic duct protruding from slit in median penal sheath. The heavily sclerotized collar at the base of the endophallic duct may be some type of pumping device.

### *Sciocorini*

#### *Sciocoris microphthalmus* (Flor), 1860

Pygophore with dorsal border widely concave (fig. 279), laterally bearing one on each side, a short stout spine; ventral border deeply emarginate medianly produced into a short square process, ventral margin flattened into a lip.

Claspers (fig. 280) with a narrow stem bearing apically a broad spatulate plate bearing a dense mat of long setae.

Theca (fig. 281) elongate narrow and cylindrical, apically expanded into a fan-like thecal shield. One pair of conjunctival appendages, basally very broad membraneous, apically divided into two lobes, a small ventral lobe with a small heavily sclerotized circular cap and a larger dorsal lobe, apically moderately sclerotized, broadly rounded and bearing a mat of stout spines (not fully expanded in diagram). Median penal lobes (fig. 282) small curved horn-like, basally fused to a common stem and enclosing apex of vesica.

Seminal duct inserted ventrally into a small anterior sinus (fig. 283); an S-shaped duct from sinus connects with a sac-like ejaculatory reservoir. Ejaculatory duct short, broadly S-shaped, apically opening between median penal lobes, basally continuous with anterior sinus.

### *Mecidini*

#### *Mecidea longula* (Stål), 1854

Pygophore and claspers described and figured by Sailer (1952).

Aedoeagus figured by Sailer (1952). Theca large and cylindrical (fig. 284). One pair of bag-like conjunctival appendages divided into dorsal and ventral lobes, dorsal lobe apically bluntly pointed; ventral lobes shorter than dorsal, apically produced into a sclerotized point. Median penal lobes (fig. 285) stout cylindrical structures, apically broadly rounded, basally fused together in a U around apex of vesica.

Ejaculatory reservoir (fig. 286) large saccular. Seminal duct opening into a wide canal ventrally; latter situated on posterior margin of reservoir and opening dorso-apically. Endophallic duct basally recessed somewhat into apex of ejaculatory reservoir, apically tapering into a short narrow duct.

**Pentatomidae - Asopinae***Zicrona caerulea* (Linnaeus), 1758

The species examined by Baker (1931) under this name has subsequently been found to be a new taxon of either specific or subspecific rank.

Pygophore with dorsal border (fig. 287) medianly evenly arched bearing two small processes one on each side dorso-laterally; ventral border (fig. 288) sinuate, bearing medianly two distinct tufts of setae borne on slight prominences. Genital plates crescent-shaped and bearing along inner margin and upper surface a number of stout peg-like teeth.

Claspers (fig. 289) simple, blade-like, apically acute.

Theca small, tubular, produced distally into a large thecal shield (fig. 290) with a deep V-shaped emargination ventrally. One pair of membranous conjunctival appendages, basally wide, apically bluntly rounded, bearing a dorsal lobe. Median penal lobes (fig. 291) broad, heavily sclerotized, basally fused.

Seminal duct (fig. 292) ventrally connected to a canal, latter encircling posterior margin of reservoir and expanding into a small chamber apically, incompletely separated from remainder of reservoir. Endophallic duct long, sinuous, basally opening into ejaculatory reservoir adjacent to seminal duct, apically terminating between median penal lobes.

Baker (1931) stated that the genital plates were absent from the species examined by him. They are in fact present, but are completely smooth.

*Oplomus tripustulatus* (Fabricius), 1803

Pygophore with dorsal border (fig. 293) gently concave with a shallow median emargination above base of proctiger. Ventral border sinuous medianly; on ventral surface is a deep heart-shaped depression. Genital plates oblong with an emargination on outer edge, surfaces ridged.

Claspers L-shaped (fig. 294) apical half blade-like, joined at right angles to stout stem.

Theca small conical, anteriorly expanded into a thecal shield (fig. 295) almost twice as large as theca, ventral margin with a wide V-shaped incision. Two pairs of voluminous membranous conjunctival appendages, both apically broadly rounded. Median penal lobes elongate plate-like (fig. 296), medianly fused, distally each produced into a long process.

Ejaculatory reservoir (fig. 297) small, globose with a canal encircling posterior surface into which seminal duct opens ventrally, canal broadens dorsally into an oval chamber communicating with reservoir. Endophallic duct long, thin and sinuous, basally entering ejaculatory reservoir adjacent to seminal duct.

*Heterosceloides lepida* (Stål), 1862

Pygophore with dorsal margin (fig. 298) deeply concave; ventral margin slightly sinuous. A large oval pit found below median section of ventral border. Genital plates P-shaped, upper surface smooth.

Claspers (fig. 299) flattened, spatulate, apical margin straight,



basally tapering to a short stout stem. Outer surface finely scalloped.

Theca small, conical, proximally produced into a thecal shield (fig. 300) with deep V-shaped emargination on ventral surface. Two pairs of conjunctival appendages: first membraneous, basally broad cylindrical, apically tapering to a blunt point; second smaller, cylindrical and membraneous, attached to a large membraneous bag-like base. Median penal lobes (fig. 301) small, flattened leaf-like structures, medianly fused, basally free and produced into two long processes.

Vesica (fig. 302) very similar to that of *Oplomus tripustulatus*, endophallic duct with a U-shaped loop anteriorly.

*Rhacognathus americanus* (Stål), 1870

Dorsal and ventral borders of pygophore (fig. 303) evenly and gently arched; genital plates small, top shaped; dorsal and ventral margins slightly crenulate.

Claspers (fig. 304) small, stem short widening into a flattened triangular apex.

Theca oblong (fig. 305), apically expanded into a thecal shield. One pair of membraneous conjunctival appendages, basally broad, apex sclerotized and acute. Median penal lobes (fig. 306) laterally oval in outline, apically free disc-like, medianly fused by means of a cross-bar, basally free and tapering.

Seminal duct (fig. 307) entering ventrally into a canal extending round posterior margin of ejaculatory reservoir and opening into a small chamber apically, latter incompletely divided by means of a septum from ejaculatory reservoir. Endophallic duct looping in a wide U, opening apically between median penal lobes, basally joining reservoir adjacent to seminal duct.

*Apateticus bracteatus* (Fitch), 1856

Pygophore and claspers (fig. 308) described by Baker (1931).

Theca oblong, produced distally into a large thecal shield (fig. 309), lateral margins sharply pointed, dorsal margin W-shaped, ventral margin broadly emarginate. One pair of very broad membraneous conjunctival appendages (fig. 309), apically produced into a stout sclerotized horn. Median penal lobes (fig. 310) oblong in shape medianly fused, basally produced into two narrow processes connected centrally by a membrane forming a hollow tube.

Vesica (fig. 311) very similar to that of *Rhacognathus americanus* but apical chamber of ejaculatory reservoir somewhat larger.

*Apateticus lineolatus* (Herrich-Schaeffer), 1839

Dorsal border (fig. 312) of pygophore with deep V-shaped emargination above proctiger; ventral margin sinuous bearing long fine setae, lying beneath ventral margin is a large oval depression part of a vertical wall between ventral border and ventral surface of pygophore. Genital plates oblong with a small pointed process on upper margin, surface with three longitudinal ridges.

Claspers (fig. 313) C-shaped, blade-like, apex acute, stem narrow.

Theca (fig. 314) small, conical, distally with thecal shield, latter rounded laterally and with a deep V-shaped cleft ventrally. One pair of membranous conjunctival appendages, apically slightly sclerotized and produced into a small sharp point. Median penal lobes (fig. 315) apically disc-like, flattened, medianly fused and distally each produced into a long narrow process.

Vesica (fig. 316) very similar to that of *Oplomus tripustulatus*, ejaculatory duct somewhat shorter.

*Podisus acutissimus* (Stål), 1870

Pygophore with dorsal border (fig. 317) broadly arched, medianly with a superior ridge bearing a small prominence (fig. 319) with a tuft of long stout setae on each side. Ventral border (fig. 318) sinuous, thickened medianly on either side of a central emargination, below this is a deep median depression. Dorsal and ventral margins covered with long fine setae. Genital plates flat, triangular, inner margin broadly scalloped with a row of scalloping behind.

Claspers L-shaped (fig. 320), stem short, stout with a broad blade attached at right angles, apically acute and finely scalloped on lower surface.

Theca small, oblong, anteriorly produced into a thecal shield (fig. 321), dorsally with a deep V-shaped emargination. One pair of membranous conjunctival appendages, basally broad, apically tapering to a blunt point. Median penal lobes thin, oblong, fused along ventral margins forming a horseshoe-like structure around the apex of the vesica.

Ejaculatory reservoir (fig. 322) with a canal extending round proximal end into an anterior chamber cut off from rest of reservoir by an incomplete septum. Seminal duct and endophallic duct entering ejaculatory reservoir adjacent to one another; endophallic duct short, sinuous; seminal duct opening directly into canal.

*Podisus maculiventris* (Say), 1899

Pygophore and claspers (fig. 323) described by Baker (1931)

Theca small, oblong, with a large thecal shield (fig. 324) evenly rounded laterally on apical margins, ventral margin V-shaped. One pair of membranous conjunctival appendages, apically tapering and blunt. Median penal lobes (fig. 325) laterally flattened, disc-shaped, basally fused.

Vesica (fig. 325) very similar in construction to *Podisus acutissimus*.

*Alcaeorrhynchus grandis* (Dallas), 1851

Dorsal border (fig. 326) of pygophore medianly evenly arched, laterally strongly curved and thickened; ventral border with a deep median U-shaped incision, beneath latter is an oval horizontal depression lined with short stout setae. Genital plates oblong, emarginate on outer border, inner margin broadly serrate.

Claspers (fig. 327) short, stout, stem apically broadened into a flat plate, upper margin emarginate.

Theca short, compact, somewhat globose, heavily sclerotized, dorsally bearing a thecal shield (fig. 328). Two pairs of conjunctival

appendages: first membraneous, wide at base, apically tapering to a heavily sclerotized point; second shorter, basally membraneous, fused to base of first appendages, apically tapering and sclerotized. Median penal lobes (fig. 329) heavily sclerotized, laterally flattened, apically free, basally fused to a common stout stem.

Ejaculatory reservoir (fig. 330) globular; seminal duct and endophallic duct entering ventrally adjacent to one another; latter long narrow and sinuous, apically opening between lateral penal lobes. Seminal duct opening into a canal extending round posterior margin of reservoir, expanding apically into a small chamber incompletely separated from rest of reservoir.

*Euthyrhynchus floridanus* (Linnaeus), 1767

Dorsal border of pygophore (fig. 331) with a shallow median emargination, genital plates lying one on either side; latter elongate narrow structures, inner margins crenulate. Ventral border with two prominent projections on either side of a median U-shaped emargination. Below ventral margin is a deep groove. Stout setae found on lateral corners of dorsal margin and ventral margin.

Claspers (fig. 332) with triangular stem, distally produced into a broad flat blade, truncate apically.

Theca small conical bearing a large rounded thecal shield (fig. 333) deeply cleft ventrally, dorsal margin U-shaped. One pair of membraneous bilobed conjunctival appendages, apices blunt; a median ventral conjunctival lobe present. Median penal lobes flattened, oblong plates, medianly united, basally each produced into a long process (fig. 334).

Vesica very similar to that of *Alcaeorrhynchus grandis*. Endophallic duct long and sinuous.

*Stiretrus anchorago* (Fabricius), 1781

Described and figured by Pruthi (1925).

Pygophore with dorsal border (fig. 335) evenly arched, ventral border with a wide median U-shaped emargination below which is a deep pit. Genital plates oblong, finely scalloped on their upper surfaces. A number of long fine setae along ventral margin.

Claspers (fig. 336) with apices flattened and hastate, attached at right angles to a slender stem.

Theca small bearing distally a large thecal shield (fig. 337) with a wide U-shaped emargination ventrally. One pair of bifid membraneous conjunctival appendages, basally wide, apically produced into two small narrow rounded processes. Median penal lobes (fig. 338) apically flattened, disc-like, centrally united around apex of vesica, basally each produced into a long process.

Vesica (fig. 339) very similar in construction to *Euthyrhynchus floridanus*. Endophallic duct long, narrow and thrown into a number of loops.

*Mineus strigipes* (Herrich-Schaeffer), 1853

Dorsal border of pygophore (fig. 340) evenly arched; ventral border with two small projections on either side of shallow median



emargination, ventral margin vertical with a wide shallow depression medianly. Genital plates large, oblong, dorsal and inner margins with 9-12 peg-like processes.

Apex of each clasper triangular (fig. 341), stem stout; apical portion of clasper bent at approximately  $120^{\circ}$  to stem, upper surface flat and bearing a series of minute scallopings.

Theca small oblong, bearing distally a thecal shield (fig. 342) with rounded lateral margins, ventrally with a deep V-shaped incision reaching margin of theca. One pair of conjunctival appendages, membranous, basally very broad, apically tapering to a blunt point. Median penal lobes elongate, bluntly pointed apically, medianly fused around apex of vesica, basally each lobe produced into a free process.

Vesica (fig. 343) very similar in construction to that of *Euthyrhynchus floridanus*, endophallic duct short.

*Perillus confluens* (Herrich-Schaeffer), 1839

No essential difference could be noted between the structure of the pygophore, aedoeagus or vesica of this species and of *Mineus strigipes*. It is probable that *Mineus* should be placed in *Perillus*, the type material would have to be examined for final decision.

*Andrallus spinidens* (Fabricius), 1787

Dorsal border of pygophore (fig. 344) steeply concave and with a superior ridge covering base of proctiger, at each end of superior ridge, is a small globose genital plate with a number of small ridges on upper surface.

Ventral border sinuous, lateral edges somewhat thickened and bearing numerous long stout setae, latter also found on outer angles and inner margin of dorsal border.

Claspers claw-shaped (fig. 345), apex acute, stem short and flattened.

Theca small, narrow with a large thecal shield (fig. 346) one and a half times as long as theca itself, enclosing conjunctival appendages, apex of each slightly sclerotized, tapering to a blunt point; dorsal to conjunctival appendages is a single membranous conjunctival lobe. Median penal lobes (figs. 347, 348) in lateral view somewhat oblong in outline, medianly fused, apically free, flattened, basally produced into two long tapering processes.

Vesica (fig. 348) very similar to that of *Rhacognathus americanus*.

## Pentatomidae - Podopinae

### *Podopini*

*Amaurochrous cinctipes* (Say), 1828

Previously described and figured by Barber and Sailer (1953).

Pygophore with dorsal border (fig. 349) evenly arched; laterally bearing two large flattened appendages (figs. 349, 350). These pygophoral appendages are the apopygeal appendages of Barber and Sailer (1953) and parandria of Leston (1953). The appendages fit into grooves on



lateral margins of pygophore, each is bluntly rounded and bears a small peg-like tooth on inner dorsal margin. Ventral border with median U-shaped emargination, on either side of which is a stout pointed process.

Claspers very characteristic (figs. 351, 352), consisting of a lower platform and an upper curved hook. A number of long stout setae on upper surface of platform and on outer surface of hook.

Theca very similar to asopine type, short, cylindrical and bearing a large thecal shield (fig. 353) not developed on ventral margin. One pair of membraneous bag-like conjunctival appendages. Median penal lobes present; oblong flattened, heavily sclerotized plates (figs. 353, 354) lying on either side of apex of endophallic duct.

Seminal duct (fig. 355) opening ventrally into a canal extending round posterior margin of large globose ejaculatory reservoir. Endophallic duct continuous with apex of reservoir, short, apically widening and opening between median penal lobes.

*Amaurochrous dubius* (Palisot de Beauvois), 1805

No difference could be noted between the genitalia of this species and of *A. cinctipes* strengthening the supposition made by Barber and Sailer (1953) that *A. cinctipes* is conspecific with *A. dubius*.

*Weda parvula* (Van Duzee), 1904

Described and figured by Barber and Sailer (1953).

Pygophore with dorsal border (fig. 356) almost straight, lateral margins bearing two large flap-like pygophoral appendages. Ventral border with a shallow median emargination on either side of which is a small broadly rounded process.

Claspers (fig. 357) small, very similar to those of *Amaurochrous cinctipes*.

Theca small, cylindrical, bearing a large thecal shield (fig. 358). One pair of membraneous balloon-like conjunctival appendages. Median penal lobes heavily sclerotized somewhat broadly hook-shaped, flattened laterally and lying on either side of vesica (fig. 359).

Ejaculatory reservoir (fig. 360) bulb-like, simple, apically continuous with a short endophallic duct; a shallow canal extends from ventro-apical entrance of seminal duct round posterior margin to dorso-apical region of ejaculatory reservoir; seminal duct opening into this canal ventrally.

*Oncozygia clavicornis* (Stål), 1872

Claspers and aedeagus figured by Barber and Sailer (1953).

Pygophore (fig. 361) very similar to that of *Weda parvula*.

Claspers biramous (fig. 362) one arm forming a blunt process, the other broadened into a flat platform bearing a fringe of long setae. Stem very short, almost non-existent.

Theca small, cylindrical bearing distally a thecal shield (fig. 363). One pair of membraneous and balloon-like conjunctival appendages. (See Sailer (1953) fig. 18, for expanded view of conjunctival appendages). Median penal lobes (fig. 365) flattened plates fused into a horseshoe-like structure (fig. 364) round apex of vesica.

Ejaculatory reservoir (fig. 366) small, globular, with a canal extending round posterior margin to dorso-apical half of reservoir. Seminal duct opening ventrally into canal; endophallic duct short sinuous, apically terminating between median penal lobes.

#### Tessaratomidae - Oncomerinae

##### *Piezosternum subulatum* (Thunberg), 1783

Pygophore with dorsal border deeply concave (fig. 367), ventral margin shallowly concave bearing medianly a heavily sclerotized oblong process. Ventral surface of pygophore produced into a large scoop-like platform projecting some way beyond the ventral margin. Outer angles of this platform with a small patch of short heavily sclerotized setae (fig. 368).

Claspers (fig. 369) simple spatulate, slightly curved. A number of long stout setae on outer apical surface.

Theca (fig. 370) squat and somewhat lopsided being produced into shield-like projection on ventral margin. Two conjunctival appendages: first heavily sclerotized, oblong, thin and flap-like lying laterally at base of conjunctiva; second lying above first, divided into two broadly rounded lobes, dorsal most lobe entirely membranous, ventral most lobe lightly sclerotized.

Vesica consisting of a long membranous tubular lobe, apically tapering to a fine needle-like point. Internally vesica very complex consisting of an ejaculatory reservoir (fig. 371) divided into dorsal and ventral chambers, connected anteriorly by means of a short spiral duct (fig. 370) and posteriorly through a wide canal. Dorsal chamber oval in outline attached directly to bases of second conjunctival appendages; ventral chamber C-shaped. Seminal duct continuous with apex of ventral chamber, extremely long thin and highly coiled tube, apically becoming straight and tapering into a very fine duct opening at apex of vesica (fig. 372).

The genitalia of this species resemble very closely those of *P. calidum* (Fabricius) described by Leston (1954), he states that there are three pairs of conjunctival appendages in *P. calidum* but does not show them on his diagram.

#### Acanthosomidae

##### *Meadorus lateralis* (Say), 1831

Pygophore (fig. 373) and claspers (fig. 374) described and figured by Baker (1931). Theca (fig. 375) squat and tub-shaped. Two pairs of conjunctival appendages: first flattened, leaf-like, slightly sclerotized; second (fig. 376) acentric, consisting of three flattened leaf-like lobes arranged around vesica, one lobe considerably longer than other two.

Seminal duct (fig. 377) opening ventrally into a globular ejaculatory reservoir, latter bearing a pair of processes on apico-dorsal surface to which bases of first conjunctival appendages are attached. Endophallic duct long, narrow and looped in a wide S, apically tapering to a very fine thread-like duct, basally merging with apex of ejaculatory reservoir.

##### *Elasmostethus cruciatus* (Say), 1831

Pygophore (fig. 378) and claspers (fig. 379) described and figured by Baker (1931).

Theca with a large rounded dorsal diverticulum (fig. 380) described as ventral by Leston (1953) for *Elasmostethus interstinctus*, squat and tub-shaped. One

pair of sclerotized, flattened and leaf-like conjunctival appendages, apically acute.

Vesica consisting of a large membranous cylindrical lobe bluntly rounded and bearing a rounded median dorsal process. Opening of ejaculatory duct diffuse, consisting of a small crenulated lobe about a third of the way up on ventral surface (fig. 381). Ejaculatory reservoir (fig. 382) found at base of vesical lobe, generally withdrawn into theca, globular and divided by means of a septum into two chambers. Seminal duct opening into posterior chamber, latter connected directly to anterior chamber. Endophallic duct long, looped basally merging into apex of anterior chamber, apically widening and forming a diffuse opening on ventral margin of vesica.

The genitalia of this species resemble very closely those of *E. interstinctus* described and figured by Leston (1953).

#### **Cydnidae - Corimelaeninae**

##### *Corimelaenini*

##### *Corimelaena pulicaria* (Germar), 1839

Pygophore with dorsal border diffuse medianly; ventral border almost straight. Pygophoral opening small surrounded by a wide flange dorsally and laterally.

Claspers very small chisel-like (fig. 384), a number of very small setae along apical margin.

Theca (fig. 385) small squat and broad, bearing a pair of spiny processes one on each side on dorsal surface near base. Laterally apical margin bears a pair of thin flat wing-like appendages one on each side. Three pairs of conjunctival appendages (not fully expanded in fig. 386): first moderately sclerotized, basally wide, tapering apically into a curved horn; second smaller, moderately sclerotized, flattened, triangular in outline, apex blunt, outer margins serrate; third chisel-like lying inside second, lightly sclerotized.

Vesica very simple. Seminal duct (fig. 387) connected ventrally to a simple saccular ejaculatory reservoir. Endophallic duct short, curved, basally merging with apex of reservoir.

#### **Cydnidae - Cydninae**

##### *Sehirini*

##### *Sehirus cinctus* (Palisot de Beauvois), 1805

Genitalia described by Froeschner (1960).

Dorsal border of pygophore (fig. 388) arched medianly, laterally sinuous; ventral border gently concave. Pygophoral opening surrounded by a wide flange.

Claspers figured by Froeschner (1960, fig. 188). Stem slender, short, bearing a narrow sickle-shaped blade; a tuft of long setae situated at base of blade.

Theca long cylindrical basally membranous, apically becoming lightly sclerotized; two small elongate heavily sclerotized flanges (fig. 389) found laterally one on each side. One pair of conjunctival appendages, membranous and bilobed.

Vesica very small lying at base of theca, consisting of a simple sac-like ejaculatory reservoir (fig. 390) which apically merges into a short straight ejaculatory duct. Seminal duct attached ventrally to base of endophallic duct, latter opening at base of a median canal formed from bases of conjunctival appendages.



The aedoeagus of this species bears no resemblance to that of *Sehirus* sp. described by Pruthi (1925).

*Cydmini*

*Pangaeus aethiops* (Fabricius), 1787

Pygophore (fig. 394), previously figured and described by Froeschner (1960).

Claspers peculiar in possessing two distinct sections (fig. 392); clasper proper (fig. 393) flattened leaf-like, outer margin with a number of long fine setae; attached to this dorsally is a tubular arm (figs. 392, 394) the function of which is unknown.

Theca (fig. 395) long, tubular, heavily sclerotized, dorsal margin produced into a lip. Three pairs of conjunctival appendages: first very small cylindrical membraneous; second fused into a membraneous tube bearing apically a pair of heavily sclerotized pads (fig. 396); third when fully inflated balloon-like, totally membraneous, apically produced into a blunt finger-like process.

Vesica very heavily sclerotized. Seminal duct (fig. 397) connecting into base of endophallic duct; a long highly convoluted duct extending from entrance of seminal duct and merging posteriorly into a saccular ejaculatory reservoir. Endophallic duct short, sinuous, basally a long duct running above convoluted duct and opening into ejaculatory reservoir. This type of vesica resembles closely the type found in the tribe Scutelleraria (Scutellerinae).

*Cyrtomenus crassus* (Walker), 1867

Dorsal margin of pygophore broad, covered with fine setae (fig. 398). Ventral margin widely U-shaped not connected with dorsal margin.

Claspers figured by Froeschner (1960). Broad flattened with a small tooth apically (fig. 399); apical margin broadly impressed bearing a large number of long fine setae; inner lateral margin with an oval area finely scalloped.

Theca cylindrical (fig. 400) very heavily sclerotized. One pair of short stout heavily sclerotized conjunctival appendages ventral to vesica.

Vesica bearing a long thin tubular infravesicular process on ventral surface (fig. 401); seminal duct opening ventrally into base of endophallic duct, latter moderately long, straight, ensheathed in a stout tapering tube. Ejaculatory reservoir flattened, tube-like, connected by means of a short spiral duct to ejaculatory duct.

*Melanaethus subglaber* (Walker), 1867

Pygophore with dorsal border broadly arched (fig. 402), ventral border gently concave. Pygophoral opening with a wide flange on dorsal and lateral margins.

Claspers figured by Froeschner (1960, fig. 243), somewhat triangular in outline with numerous hairs on thickened apical margin.

Theca (fig. 403) elongate, tubular. Two pairs of conjunctival appendages: first basally membraneous, apically heavily sclerotized



and blunt; ventralmost appendages (probably third) (fig. 404) basally fused, apically produced into two small broadly rounded lobes, sclerotized throughout.

Vesica small; seminal duct (fig. 405) connected ventrally to base of ejaculatory duct; latter a short straight tube surrounded by a stout sheath, tapering apically; basally endophallic duct merging into an unusual spiral ejaculatory reservoir.

*Amnestini*

*Amnestus pallidus* (Zimmer), 1910

Pygophore with dorsal border evenly arched (fig. 406), ventral border concave. Pygophoral opening surrounded by a wide flange.

Claspers (fig. 407) with a short narrow stem, widening medianly, apically produced into an acute point. A number of fine setae scattered over outer surface of clasper.

Theca (fig. 408) small, membranous, globose. Two pairs of conjunctival appendages (fig. 409): first divided into two pairs of small spikes, apically slightly sclerotized; second, large bag-like, lightly sclerotized (probably balloon shaped when fully inflated). All appendages attached to fairly voluminous conjunctiva.

Seminal duct (fig. 410) very fine, opening ventrally into a long canal at apex of vesica; canal merging into an internal duct opening into ejaculatory reservoir. Endophallic duct long, basally merging with apex of central sinus.

## DISCUSSION

The major work dealing with the male genitalia of North American pentatomids is that of Baker (1931). However he dealt with Canadian species of Pentatominae and Asopinae only. Recently, Lattin (1964) has examined the male genitalia of all North American Scutellerinae and thereby filled a large gap in our knowledge. Pruthi (1925) worked with the world Hemiptera; his findings are of limited value in some taxa, because only a very small number of species was examined. This gave an inaccurate view of some groups. Several other workers have dealt with the male genitalia of a small number of species of various families within the Pentatomoidea. These papers have been considered in the present study wherever relevant.

### **Pentatomidae - Scutellerinae**

The male genitalia amongst species of North American scutellerines are very varied and difficult to assess. The tribe Eurygastrini, as constituted by Leston (1952), included three subtribes: Eurygastraria, Odontoscelaria and Odontotarsaria. Lattin (1964) has separated the Eurygastraria from the rest of this group on the basis of the male genitalia and accorded it tribal status.

The European species of Eurygastrini, possess very uniform characters, Wagner (1963), Vidal (1949) and Piotrowski (1950). Most

members of this tribe have the following features in common: T-shaped claspers, two to three pairs of heavily sclerotized horn-like conjunctival appendages and a cylindrical membranous vesica. Unfortunately details of the internal structure of the vesica have not been considered by other workers in this field so far. The internal details of the vesica of *Eurygaster alternatus* are definitely pentatomid (fig. 26) and do not resemble the type found in the Scutelleraria. The ejaculatory reservoir is simple and is connected directly via an anterior sinus to the seminal duct and ejaculatory duct.

The remaining members of the tribe Eurygastrini are now included in the Odontoscelini. The male genitalia of the four North American species show remarkably little similarity to one another with the exception of *Euptychodera corrugata* and *Fokkeria producta*. This relationship can be seen in figure 520, which is an analysis of eleven character differences found in males and females based on the method of James (1953). Three species all possess stout spiny conjunctival appendages; the vesica of *Homaemus aeneifrons* is, however, quite different from the other two.

The tribe Pachycorini is represented in North America by ten genera, of remarkably uniform character. They have two patches of fine striae on abdominal sterna four to six, one on each side of the midline. Outside of the New World only *Hotea* and *Deroplax* (Leston, 1952) and female *Tectocoris* (Lattin, 1964) possess this character. *Hotea* and *Deroplax* are central African in distribution; *Tectocoris* is Australian.

The male genitalia of this tribe show a remarkable array of different types of structure. The analysis of character differences (fig. 520) shows that the species in this group are very variable. *Homaemus aeneifrons* has been discussed above under Odontoscelini. The remaining species show two trends as far as the structure of the vesica is concerned. The ejaculatory reservoir is absent or very small in most; the second group generally has a large S-shaped ejaculatory reservoir and in *Stethaulax marmoratus* and *Camirus moestus* a convoluted duct typical of the Scutellerini. The Australian species *Tectocoris diophthalmus* (McDonald, 1961) is quite aberrant in possessing a very small tube-like ejaculatory reservoir. The conjunctival appendages vary in number from one to three pairs, however the third when present is never heavily sclerotized and S-shaped as in the Scutelleraria. Claspers are hook-shaped, except in *Symphylus caribeus*, where they are T-shaped.

*Augocoris gomesii* has very clear cut characters, possessing a convoluted thickened duct, hook-shaped claspers, sclerotized S-shaped third conjunctival appendages and a short stout endophallic duct and is typical of other members of the Scutellerini and quite distinct from other species examined (fig. 520). *Augocoris* also shows very great similarity to Australian members of this tribe in the structure of its aedoeagus (McDonald, 1961, 1963) and vesica (Kumar, 1964).

#### Pentatomidae - Pentatominae

As stated in the introduction both Baker (1931) and Pruthi (1925) dealt with this subfamily in some detail. In the tribe Pentatomini, containing the vast majority of the species in North America, five species were found to possess an enormously lengthened endophallic duct which

is coiled like a watch spring. This type of genitalia was described by Baker (1934) but not commented on. The other group containing all other species studied has a relatively short endophallic duct.

All species possessing elongate coiled endophallic ducts have several characters in common. All have a pair of dorsal thecal processes (titillators of Baker, 1931), one or two membraneous conjunctival appendages and a pair of heavily sclerotized median penal lobes fused into a flat circular structure with a dorsal median groove. The ejaculatory reservoir is heavily sclerotized, consisting of two chambers divided by means of an internal septum and with the exception of *Euschistus tristigmus* bear a number of transverse striae on the sides.

The other group of species does not present such a uniform picture. Claspers vary greatly and have many forms. Five species were found to have a thecal shield (an asopine character) and of these, *Loxa flavicollis*, has such peculiarly constructed claspers (fig. 226) and aedoeagus (fig. 228) that its inclusion in this tribe is suspect. The remaining four species all have one pair of membraneous conjunctival appendages, a pair of median penal lobes and a simple sac-like ejaculatory reservoir with a posterior canal, all characters possessed by the Asopinae. However, none of these species have genital plates.

*Carpocoris remotus*, *Dendrocoris humeralis*, and *Pentatoma rufipes* all have genital plates, one pair of membraneous conjunctival appendages and a simple ejaculatory duct. However, all lack a thecal shield. Both these groups thus connect the asopines very closely to the Pentatomini.

The other species examined in this grouping generally had one or two conjunctival appendages varying greatly in shape. The ejaculatory reservoir is simple, generally with the seminal duct opening into a posterior canal. The endophallic duct varies greatly in its length and shape. Median penal lobes, usually present, are absent from five species.

Piotrowski (1950), Kumar (1962) and Pruthi (1925) have all described and figured the male genitalia of Pentatominae except for the vesica. The structure of the aedoeagus varies. Kumar (1964) has figured the vesicae separately of eight species of Pentatominae, their structure agrees closely with those of North American species (one, *Nezara viridula* occurs both in Australia and North America). Leston (1952) states that the genitalia of *Deroplax circumducta* (Scutellerinae) are like the typical Pentatomid genitalia in possessing a long thin vesica surrounded by the conjunctiva. This is not correct since the type of the family *Pentatoma rufipes* has a short stout vesica and only one genus so far examined, *Trichopepla semivittata*, has anything like an elongate, thin vesica. So far the only genera possessing the extraordinary elongated coiled endophallic duct are North American (Baker 1934).

Investigation of the remaining tribes within the Pentatominae is limited to single genera, and comments on these are therefore rather speculative. The genitalia of the two species of *Brochymena* examined are so similar to those found generally among the Pentatomini that the validity of the Halyini is suspect.

The genitalia of the genus *Mecidea* were studied in detail by Sailer (1952). The aedoeagus is very similar to that found among the Pentatomini and is remarkably constant for the group in possessing two pairs of bag-



like membraneous conjunctival appendages and a pair of median penal lobes. The vesica is very simple in construction and resembles the general pattern found among the majority of Pentatomini. Once again on the basis of genitalia the elevation of this genus to tribal level is unwarranted.

The remaining tribes, Edessini, Discocephelini and Sciocorini all show certain characteristics peculiar to the species studied. Until more work has been done, little can be said on the status of these tribes except that they all share characters with the Pentatomini.

#### **Pentatomidae - Asopinae**

Baker (1931) described the Canadian species of this subfamily. The following characters are common to all the species examined by myself and to those described in the literature.

1. Pygophore with a pair of genital plates on the dorsal margin, one on each side. 2. Theca with apical margin developed into a thecal shield. 3. Conjunctival appendages variable in number but always membraneous. 4. Median penal lobes present and enclosing the apex of the vesica. 5. Ejaculatory reservoir simple with seminal duct entering a posterior canal. Endophallic duct and seminal duct enter reservoir adjacent to one another.

The male genitalia show remarkable constancy in this group.

The Asopinae are differentiated on minor character differences externally, but can now, on the basis of the male genitalia, be very clearly defined. The general structure of the male genitalia is similar to that found in the Pentatomini discussed above.

Leston (1954a) describes and figures the genitalia of *Afrius figuratus* (Germar) a species from Africa which also clearly possesses the characters set out above. The genital plates are termed dorsal processes by Leston. The status of the Asopinae will be discussed later.

#### **Pentatomidae - Podopinae**

The North American species were revised by Barber and Sailer (1953). The aedoeagus of four species is figured, but not the internal structure of the vesica. The genitalia of this subfamily are rather uniform; the following characters were found to be common to all species so far examined. 1. Lateral margins of pygophore with a pair of appendages. 2. Theca with a thecal shield. 3. One pair of membraneous conjunctival appendages. 4. A pair of median penal lobes. 5. Ejaculatory reservoir simple, with a posterior canal.

Leston (1953a) described the genitalia of *Podops inuncta* (Fabricius) and they fit the general pattern found among North American species. The Podopinae are very closely related to the Asopinae, the former subfamily lacking genital plates. Their place seems to have been taken by the pygophoral appendages.

The Podopinae like the Asopinae are thought to be closely related to the Pentatominae. Leston (1953a) noted this when he raised this group to subfamily status.



### Tessaratomidae

Leston (1954c, 1954d, 1957) and Pruthi (1925) have both described the male genitalia of this family. Only one species *Piezosternum subulatum*, is described here. The genitalia of this species and of *Piezosternum calidum* (Fabricius) (Leston 1954c), an African species, are very similar. Both possess very long and highly convoluted endophallic ducts (the vesica does not appear to be fully expanded in Leston's diagram), and one pair of heavily sclerotized conjunctival appendages. *Elizabetha courteaui* Schouteden (Leston, 1954c) and *Phyllocoris acuta* Jeannel also have very long endophallic ducts. However the Australian species *Musgravea sulciventris* (Stal) and *Rhoecocoris australasiae* (Westwood) do not have elongate endophallic ducts (Leston, 1957). Kumar (1964) studied the vesicae of four Australian tessaratomids. None have the elongate endophallic duct of *Piezosternum subulatum*; all, however, including *Piezosternum*, have a complicated series of canals within the ejaculatory reservoir (conducting chamber of Kumar). It would appear on the basis of the male genitalia that the subfamily Oncomerinae should be split into two or more sub-families. Leston (1955) suggested that *Piezosternum* might have to be removed from the Oncomerinae.

Leston (1954d) described the genitalia of *Tessaratoma papillosa* (Drury). These agree closely with *Tessaratoma* sp. figured by Pruthi (1925). The endophallic duct is short and two pairs of membraneous conjunctival appendages are present relating this tessaratomine to the Australian species of Oncomerinae. Other species figured and described by Pruthi (1925) from the Eustheninae show close similarities to the Tessaratominae but not to *Piezosternum*.

### Acanthosomidae

Very little work has been done on the male genitalia. Leston (1953b) describes and figures *Cyphostethus tristriatus* (Fabricius) and *Elasmotethus interstinctus* (Linnaeus). Only two species were examined in the present work, *Meadorus lateralis* and *Elasmotethus cruciatus*. All species with the exception of *Meadorus lateralis* have a peculiar dorsal diverticulum on the theca and all have at least one pair of flattened sclerotized conjunctival appendages. However *Cyphostethus* and *Meadorus* have elongate whip-like endophallic ducts whereas both species of *Elasmotethus* have rather apically diffuse endophallic ducts. The ejaculatory reservoir in both species examined by me were pentatmoid in construction, being simple sacs with a dorsal canal, the endophallic duct passing out apically. Leston did not, unfortunately, examine the internal structure of the vesica of the two specimens he describes.

### Cydnidae

A very extensive study was made on the European species of this group by Wagner (1963). The present study is rather cursory and will indicate certain trends among species of the North American fauna. Wagner did not consider the vesica, so no comparisons of this structure can be made.

### Cydnidae - Corimelaeninae

The pygophore of *Corimelaena pulicaria*, the only species of this subfamily examined, resembles that described by Wagner (1963) for *Corimelaena scarabaeoides*. The aedoeagus of this latter species differs from that of *C. pulicaria* in possessing only two pairs of heavily sclerotized horn-like conjunctival appendages (Wagner's spicula). Three pairs of conjunctival appendages were found in *C. pulicaria* (fig. 386) and were quite different in shape from those of *C. scarabaeoides*. McAtee and Malloch (1933) figured the aedoeagus of twelve corimelaenines. All possessed two to three pairs of stout sclerotized appendages, five possessed the wing-like appendages on the margin of the theca.

### Cydnidae - Cydninae

Wagner (1963) recognizes two major types of genitalia in this subfamily, the *Geotomus* type and the *Sehirus* type. One species only, *Sehirus cinctus*, of the tribe Sehirini exists in North America. On examination, the male genitalia of this species proved to be quite different from any of the genitalia described by Wagner for species in this tribe. The European species all possessed at least one pair of heavily sclerotized conjunctival appendages, generally rod-like. The claspers show striking similarity being somewhat Y-shaped. *Sehirus cinctus* has only one pair of membraneous conjunctival appendages (fig. 389) and the claspers are large and sickle-shaped. I note here that the vesicae of *Sehirus cinctus* and *Corimelaena pulicaria* are very similar.

Froeschner (1960) recognized *Amnestus* as a separate subfamily. One species, *Amnestus pallidus*, Zimmer was examined. The vesica is unusual in possessing a very long canal into which the seminal duct opens apically (fig. 440); the canal passes back into the ejaculatory reservoir.

Wagner's (1963) *Geotomus* type genitalia characterized by the possession of two pairs of conjunctival appendages, and a moderately long endophallic duct, although he notes that the genus *Cydnus* is aberrant. The three species of North American Cydnini studied, show great variation in the aedoeagus and vesica. The number of conjunctival appendages varied from one pair in *Cyrtomenus* (fig. 400) to three in *Melanaethus* (fig. 403). The vesica of *Pangaesus aethiops* is very similar to that found in the Scutellerini, in possessing a long convoluted duct. *Aethus indicus* and *Geotomus apicalis* (described by Kumar 1962) have an infra-vesicular process also found in *Cyrtomenus crassus* (fig. 401). The structure of the ejaculatory reservoir and associated ducts is very similar both in *Geotomus apicalis* and *Cyrtomenus crassus*. *Aethus indicus* was shown to have three pairs of conjunctival appendages (Kumar 1962) and a convoluted duct, characters shared in common with *Pangaesus aethiops*. However, the latter species lacks the infra-vesicular process. Wagner (1963) figures an extremely long coiled endophallic duct for *Chilocoris* spp. and *Cydnus aterrimus* Forst. In the latter species the duct is coiled at the base of the theca. This condition was not observed in any of the North American species examined. It is unfortunate that Wagner (1963) did not deal with the structure of the ejaculatory reservoir. From his work it would appear that the Sehirini, except for the North American species, is a good grouping and resembles the Eurygastrini (Scutellerinae) in the structure of the aedoeagus. Leston

(1954b) describes the genitalia of *Sehirus bicolor* and in another paper Leston (1956) describes two species of *Dismegistus*. All these species possess three pairs of conjunctival appendages, the third lightly sclerotized, and an endophallic duct projecting well beyond the margin of the theca. Wagner (1963) apparently only found two conjunctival appendages (spicula) in members of this tribe. It is clear that further work is required on species included in this tribe. *Sehirus cinctus* (fig. 389) has only one pair of membranous bifid appendages and a very short vesica not projecting beyond the margin of the theca and the aedoeagus in no way resembles that of *Sehirus bicolor*. It would appear that on the basis of the male genitalia *Sehirus cinctus* is wrongly placed with the Old World species.

### MORPHOLOGY OF FEMALE GENITALIA

The female genitalia are not as complex as those of the male. Detailed diagrams and descriptions are not given for each species since the genitalia generally vary in broad characteristics only. Scudder (1959) has described the genitalia of this group fully and any divergence from his general descriptions has been noted. The spermatheca of each species was studied in more detail and provides some useful characters which give some good clues to the relationships of the various groups.

The female genitalia are situated on abdominal segments eight and nine and are of the plate-shaped type with a posterior or postero-ventral aspect. The paratergites of segments eight and nine, together with the first gonocoxae (segment 8), form the major part of the external genitalia. The second gonocoxae (segment 9) generally form a bridge-like sclerite beneath sternum 10. The gonapophyses attached to the gonocoxae are generally membranous. The gonangulum is fused posteriorly to tergum 9. In some species the dorsal edge of the first gonapophysis is heavily sclerotized and forms the grooved outer ramus. The ventral edge of the second gonapophysis is in some species also heavily sclerotized and forms the inner ramus.

#### Pentatomidae - Scutellerinae

##### *Odontoscellini*

Genitalia externally plate-like, very similar in all species. Descriptions are given by several authors, detailed descriptions will not be included here.

*Fokkeria producta* (Van Duzee), 1904. (figs. 411, 412)

*Euptychodera corrugata* (Van Duzee), 1904

Genitalia of these two species almost identical. Genital chamber with a deep median sclerotized groove (fig. 413) at dorsal end of which is a small membranous pouch, into which spermatheca opens. Spermathecal duct long, leading into a pumping region, poorly defined from spermathecal bulb, proximal flange of pump developed (fig. 414), lightly sclerotized. The shape of the spermathecal bulb differs in the two species, being somewhat more elongate in *Fokkeria* than in *Euptychodera*.



*Vanduzeeina balli* (Van Duzee), 1904

Very similar (fig. 445) to *Fokkeria producta*, spermathecal duct long (fig. 446), membranous, spermathecal bulb elongate cylindrical.

*Phimodera binotata* (Say), 1824

Entrance of spermatheca into genital chamber surrounded by a circular sclerite (fig. 448); a short groove extending along base of chamber from this sclerite.

Spermathecal duct short, opening into a large tough sac-like dilation (fig. 447); from latter a short duct connects to pumping region with proximal flange only developed. Spermathecal bulb dumb-bell shaped.

*Eurygastrini**Eurygaster alternata* (Say), 1828

External genitalia flattened and facing ventrad, similar to Pentatomine type. Internally a pair of sclerotized interlocking rami present, similar to those found in Scutellerini (McDonald 1963). Second gonocoxae lightly sclerotized elongate plates, not fused centrally. Genital chamber with a long sclerotized groove (fig. 449).

Spermathecal duct short; pumping region with flanges indicated only by slight swelling for muscle attachment; spermathecal bulb spherical, separated from pump by a short duct. This species is quite distinct in possessing sclerotized rami.

*Pachycorini*

The external genitalia are essentially very similar. Minor differences exist among species and these are described.

*Pachycoris torridus* (Scopoli), 1722

Visible portion of first gonocoxae reduced, bases hidden beneath seventh sternum. Opening of spermatheca (fig. 420) into genital chamber surrounded by a heart shaped sclerite; a deep median sclerotized groove extending along length of genital chamber from this sclerite. Spermathecal duct with a large spherical dilation (fig. 421) pumping region small with distal and proximal flanges developed, spermathecal bulb elongate cylindrical.

*Diolcus irroratus* (Fabricius), 1775

Genital chamber with a narrow, heavily sclerotized groove (fig. 423), anteriorly opening into a heavily sclerotized pouch (fig. 442), into which spermatheca opens; spermathecal duct short, stout, dilating into a thick walled chamber (fig. 424) from which apically a short membranous duct leading to a pump, with proximal flange only developed; spermathecal bulb elongate cylindrical.

*Tetyra antillarum* (Kirkaldy), 1909

First gonocoxae (fig. 425) each with a large sclerotized base projecting internally beneath sternum seven. A large anchor-shaped sclerite (fig. 426) present around opening of spermatheca into genital



chamber. Spermathecal duct narrow, membraneous, with a large membraneous sac-like diverticulum, pumping region small, proximal and distal flanges (fig. 427) developed; spermathecal bulb globose connected by a short duct to pump.

*Symphylus caribeanus* (Kirkaldy), 1909

A long, heavily sclerotized plate-like sclerite extending along base of genital chamber (fig. 428) from entrance of spermatheca. Spermathecal duct basally broad expanding into a globular dilation, from which a narrow duct connects to pumping region; latter with both flanges developed and connected by means of a moderately long, stout duct to a spherical spermathecal bulb.

*Sphyrocoris obliquus* (Germar), 1839

Very similar to *Homaemus aeneifrons*.

Dilation smaller, pumping region not clearly differentiated (fig. 429), proximal flange only developed. Spermathecal bulb continuous with pump, elongate cylindrical (fig. 430).

*Homaemus aeneifrons* (Say), 1824

Sclerotized groove (fig. 431) present in base of genital chamber. Spermathecal duct marked by numerous annulations; pumping region (fig. 432) poorly defined, proximal flange present, membraneous; distal flange missing; spermathecal bulb elongate, S-shaped.

*Acantholomidea porosa* (Germar), 1839

Eighth paratergites absent, ninth narrow and elongate (fig. 433). Spermatheca opening into base of heavily sclerotized groove (fig. 434) lying in base of genital chamber; a sac-like spermathecal diverticulum also opening into this groove adjacent to spermathecal entrance. Spermathecal duct medianly with a sac-like dilation, pumping region small, with proximal flange only developed; spermathecal bulb elongate and rod-like (fig. 435).

*Cheylsomidea guttata* (Herrich-Schaeffer), 1839

First gonocoxae (fig. 436) triangular, smaller than other species examined in this tribe; internally a pair of sclerotized outer rami (fig. 436) present. Spermatheca opening into a pouch (fig. 437) with a heavily sclerotized groove. Spermatheca minute, duct long, narrow passing to a small pumping region (fig. 438), proximal flange reduced, distal flange present, spermathecal bulb elongate sausage-like.

This species is distinct from other members of this tribe in possessing one pair of rami.

*Stethaulax marmoratus* (Say), 1831

A long heavily sclerotized groove extending along base of genital chamber (fig. 440) from spermathecal opening. Spermathecal duct long, with a large saccular diverticulum (fig. 441) attached mid-way; pumping region small (fig. 442), proximal flange well developed, distal flange very small; spermathecal bulb oval connected to pump by a short duct.

*Scutellerini*

*Augocoris gomesii* (Burmeister), 1835

External genitalia plate-like, typically Scutellerine (Scudder, 1959). Sclerotized and interlocking rami present.

Spermatheca typical for members of this tribe. Spermathecal duct (fig. 443) medianly expanded into a heavily sclerotized globular chamber with a series of fine markings externally; pumping region well developed connected to spermathecal dilation by a short duct; spermathecal bulb elongate apically expanded into a spherical bulb. This species is very similar to other members of this tribe in possessing sclerotized rami (Scudder 1959, McDonald 1963) and the large sclerotized median dilation of the spermathecal duct (Pendergrast 1957).

**Pentatomidae - Pentatominae**

The external genitalia are all very similar in this sub-family and are described by Scudder (1959). The presence or absence of spiracles on the eighth paratergites varies from species to species. Sclerotized rami are lacking, ring sclerites were found in the two European species studied, *Pentatoma rufipes*, and *Eysarcoris aeneus*.

The spermatheca has been described by Pendergrast for several species and is remarkably constant. The spermathecal duct is expanded into a large elongate balloon-like dilation (fig. 474) down the centre of which is a sclerotized rod varying in thickness from species to species. The apex of this rod is free and a narrow channel extends down the centre and basally emerges from the diverticulum as a narrow duct connecting with the pumping region and spermathecal bulb. The pumping region has well defined proximal and distal flanges for the insertion of muscles and is attached directly to the spermathecal bulb. The shape of the latter varies somewhat but in the majority of species is spherical or oval. One exception only to this general pattern was found, in *Trichopepla semivittata* the spermatheca consists of a long duct terminating in a membraneous sac with no differentiation of pumping region or bulb (fig. 476).

Any variation from the general pattern described above will be noted under each specific description.

*Pentatomini*

*Rhytidolomia senilis* (Say), 1831. (figs. 444, 445)

*Rhytidolomia viridicata* (Walker), 1867. (fig. 446)

*Rhytidolomia saucia* (Say), 1831

*Chlorochroa ligata* (Say), 1831

Eighth paratergites with spiracles. Second gonocoxae fused into a single plate. Second gonapophyses found above the spermathecal entrance (fig. 444) and two small sclerites surround the opening of the spermatheca into the genital chamber. Spermatheca as described above.

*Banasa dimidiata* (Say), 1831. (fig. 447)

*Carpocoris remotus* (Horvath), 1907. (fig. 448)

*Murgantia histrionica* (Hahn), 1834. (figs. 449, 450)

*Padaeus viduus* (Vollenhoven), 1868

.Eighth paratergites with spiracles. Two small sclerites surrounding opening of spermatheca. In case of *Murgantia histrionica*, these sclerites are somewhat larger (fig. 450), the ventralmost sclerite forming a platform and the smaller dorsal sclerite forming a spout round the spermathecal opening. Spermatheca normal, shape of spermathecal bulb varies from species to species.

*Mormidea lugens* (Fabricius), 1775

*Euschistus tristigmus* (Say), 1831. (fig. 452)

*Hymenarcys nervosa* (Say), 1832

*Cosmopepla bimaculata* (Thomas), 1865. (figs. 453, 454)

*Menecles insertus* (Say), 1831

*Brepholoxa heidemanni* (Van Duzee), 1904. (figs. 455, 456)

*Dendrocoris humeralis* (Uhler), 1877. (fig. 457)

*Coenus delius* (Say), 1831

*Eysarcoris intergressus* (Uhler), 1893

*Prionosoma podopioides* (Uhler), 1863. (figs. 458, 459)

*Solubea pugnax* (Fabricius), 1775. (figs. 460, 461)

Eighth paratergites without spiracles. Entrance of spermatheca surrounded by one or two small sclerites. Spermatheca as described under general heading, shape of spermathecal bulb varies in each species as does the size and shape of the flanges of the pumping region.

*Neottiglossa trilineata* (Kirby), 1837. (fig. 462)

*Loxa flavicollis* (Drury), 1773. (fig. 463)

*Nezara viridula* (Linnaeus), 1758

*Arvelius albopunctatus* (DeGeer), 1773. (figs. 464, 465)

*Aelia americana* (Dallas), 1851. (fig. 466)

*Acrosternum pennsylvanicum* (DeGeer), 1773. (figs. 467, 468)

*Peribalus limbolarius* (Mulsant and Rey), 1866. (figs. 469, 470)

*Vulsirea violacea* (Fabricius), 1803. (figs. 471, 472)

*Pentatoma rufipes* (Linnaeus), 1758. (figs. 473, 474)

*Chlorocoris subrugosus* (Stal), 1872. (fig. 475)

All the above species are characterized by the fact that the spermathecal bulb has from 2-4 hollow horn-like processes (fig. 474) on it, these vary in size and shape being long and slender in *Chlorocoris subrugosus*, small and squat in *Peribalus limbolarius*. *Nezara viridula* has been described and figured by Pendergrast (1957). The spermatheca is otherwise normal in possessing a median dilation with central sclerotized rod, spermathecal opening surrounded by one or two sclerites. *Pentatoma rufipes* has in addition ring sclerites, this species is palaearctic in distribution. Spiracles may be present or absent.

*Peribalus limbolarius* (fig. 461), *Nezara viridula*, *Aelia americana* (fig. 466), *Acrosternum pennsylvanicum* (fig. 468) and *Pentatoma rufipes* all possess two processes on the spermathecal bulb.

*Neottiglossa trilineata*, *Chlorocoris subrugosus*, *Loxa flavicollis* (fig. 463) and *Arvelius albopunctatus* possess three appendages. *Vulsirea violacea* has four appendages.

The function of these processes is unknown.



*Trichopepla semivittata* (Say), 1832

Eighth paratergites with spiracles. First gonapophyses sclerotized. Spermatheca simple consisting of a narrow duct terminating in a simple membraneous sac (fig. 476), no pumping region present.

*Proxys punctulatus* (Palisot de Beauvois), 1805

Eighth paratergites without spiracles.

Spermathecal dilation constricted anteriorly (fig. 477) giving it a bottle shape, otherwise spermatheca similar to standard description.

*Thyanta perditor* (Fabricius), 1794

Eighth paratergites with spiracles. A small circular sclerite surrounding opening of spermatheca. Spermathecal dilation (fig. 478) elongate bearing proximally a bulbous cap within which sclerotized rod expanded into a bell shaped apex. Proximal to pumping region, duct swollen into a sclerotized bulb (fig. 479) with a number of transverse ridges, spermathecal bulb very elongate rod-like.

*Eysarcoris aeneus* (Scopoli), 1763

Eighth paratergites without spiracles. Two ring sclerites (fig. 480) present one on either side of a V-shaped sclerite surrounding spermathecal opening. Spermathecal dilation constricted proximally forming a large distal chamber and a smaller more elongate proximal chamber, spermatheca otherwise normal.

This is a European species and shows marked differences from the American species *Eysarcoris intergressus* as noted in the description of the male genitalia.

*Halyini**Brochymena quadripustulata* (Fabricius), 1775*Brochymena arborea* (Say), 1825

Eighth paratergites with spiracles. First gonapophyses sclerotized; second gonocoxae fused plate-like. Opening of spermatheca surrounded by two sclerites (fig. 481). Spermathecal bulb with two processes in *Brochymena quadripustulata*; *B. arborea* with an additional small third appendage. Spermatheca in other respects similar to general description under Pentatomini.

*Edessini**Edessa bifida* (Say), 1832

Eighth paratergites with spiracles; second gonocoxae fused. Spermatheca similar to *Brochymena quadripustulata* spermathecal bulb with three processes of equal size (fig. 482)

*Sciocorini**Sciocoris microphthalmus* (Flor), 1860

Eighth paratergites without spiracles, external genitalia typically

Pentatomine in character. Base of spermathecal duct surrounded by a small horseshoe shaped sclerite (fig. 483) with a second crescent shaped sclerite in front of it, spermatheca as described under Pentatomini.

#### *Discocephalini*

##### *Lineostethus clypeatus* (Stål), 1862

Eighth paratergites with spiracles. Ninth paratergites small oval structures; second gonocoxae fused, narrow. Entrance of spermatheca surrounded by a small circular sclerite, otherwise similar to *Sciocoris microphthalmus*, duct from spermathecal dilation to pumping region wider, longer and convoluted (fig. 484).

#### *Mecidini*

##### *Mecidea longula* (Stål), 1854

Eighth paratergites with spiracles, ninth vertical, projecting beyond posterior margin (fig. 485); spermatheca similar to *Sciocoris microphthalmus*.

#### **Pentatomidae - Asopinae**

*Mineus strigipes* (Herrich-Schaeffer), 1853. (figs. 486, 487)

*Rhacognathus americanus* (Stål), 1870. (fig. 488)

*Oplonus tripustulatus* (Fabricius), 1803

*Andrallus spinidens* (Fabricius), 1787

*Podisus acutissimus* (Stål), 1870. (figs. 489, 490)

*Podisus maculiventris* (Say), 1899. (fig. 491)

*Apateticus lineolatus* (Herrich-Schaeffer), 1839. (fig. 492)

*Stiretrus anchorago* (Fabricius), 1781

*Heterosceloides lepida* (Stål), 1862

*Perillus confluent* (Herrich-Schaeffer), 1839. (fig. 493)

*Alcaeorrhynchus grandis* (Dallas), 1851. (fig. 494)

*Euthyrhynchus floridanus* (Linnaeus), 1767. (fig. 495)

*Zicrona caerulea* (Linnaeus), 1758. (figs. 496, 497)

All the above species were examined and present a remarkably uniform picture in the structure of the female genitalia and agree with the general description given by Scudder (1959) for Pentatomidae.

The spermathecae were also extremely uniform and resemble *Hoploxys coeruleus* Dallas figured by Pendergrast (1956). Minor variations in the size and shape of the spermathecal bulb were found. Eighth paratergites with spiracles, second gonocoxae fused (figs. 486, 496), heavily sclerotized and visible externally as a trapezoidal plate; no rami present.

Spermatheca of typical Pentatomine construction. One or two small sclerites found round the entrance of the spermatheca into the genital chamber (fig. 492); medianly spermatheca dilated into an elongate chamber down the centre of which runs a heavily sclerotized rod, a narrow duct passing along centre of rod and out of dilation to a well developed pumping region with proximal and distal flanges, spermathecal bulb attached directly to pump, varying in shape from species to species (see

figures).

*Euthyrhynchus floridanus* is unique in possessing a pair of ring sclerites one on either side of the spermathecal opening, also the distal flange is absent in the pumping region, otherwise similar to previous species.

#### **Pentatomidae - Podopinae**

##### *Podopini*

*Amaurochrous dubius* (Palisot de Beauvois), 1805

*Amaurochrous cinctipes* (Say), 1828

Genitalia typically Pentatomine in construction. Eighth paratergites ventrally not fused, without spiracles (fig. 498). Spermathecal bulb with three processes (fig. 499) spermatheca otherwise similar to that described under Pentatomini.

*Weda parvula* (Van Duzee), 1904

Genitalia and spermatheca very similar to preceding species, spermathecal bulb with two processes only (fig. 500).

#### **Tessaratomidae - Oncomerinae**

*Piezosternum subulatum* (Thunberg), 1783

Eighth and ninth paratergites long apically acute sclerites (fig. 501), eighth with spiracles. Sclerotized and paired ramipresent, second gonocoxae fused plate-like; second gonapophyses partially sclerotized. Ring sclerites present (fig. 502), also noted by Scudder (1959) in *Piezosternum calidum*.

Spermathecal duct wide on entrance into genital chamber, slightly sclerotized at base, long, coiled, terminating in a pumping region with proximal and distal flanges; spermathecal bulb heavily sclerotized oval in shape attached directly to pump. The spermatheca of this species differs from *Musgravea (Rhoecocoris) sulciventris* figured by Pendergrast (1956), also a member of the Ocomerini, in not possessing a spermathecal diverticulum but does resemble the other three species figured.

#### **Acanthosomidae**

*Elasmotethus cruciatus* (Say), 1831

External genitalia similar to *Acanthosoma haemorrhoidale* described by Scudder (1959), tenth sternum divided (fig. 503); paired and sclerotized rami present.

A small sclerotized groove found in floor of genital chamber extending between entrance of spermatheca and that of oviduct. Spermatheca (fig. 504) consisting of a narrow duct terminating in a pumping region with proximal and distal flanges; spermathecal bulb cylindrical.

*Meadorus lateralis* (Say), 1831

Genitalia and spermatheca (fig. 505) very similar to *Elasmotethus cruciatus*; eighth paratergites divided; distal and proximal



flanges of pump well developed.

### **Cydnidae - Corimelaeninae**

#### *Corimelaenini*

##### *Corimelaena pulicaria* (Germar), 1839

Paratergites eight fused centrally (fig. 506); two pairs of elongate sclerites visible above the large flap-like first gonocoxae, tenth sternite being dorsalmost, ninth paratergites lying beneath. Second gonocoxae not visible externally. No sclerotized rami or ring sclerites present.

Spermatheca (fig. 507) consisting of a simple duct connecting to pumping region with proximal flange only developed; spermathecal bulb mushroom shaped, attached directly to pump.

##### *Galgupha nitiduloides* (Wolff), 1802

External genitalia very similar to *Corimelaena pulicaria*. No sclerotized rami.

Spermatheca very similar to that figured and described by Pendergrast (1957) for *Galgupha ovalis* Huss, shape of spermathecal bulb differs somewhat (fig. 509). Two accessory sacs present one on either side of spermathecal entrance (fig. 508), their function unknown; spermathecal opening into a narrow sclerotized groove.

### **Cydnidae - Cydninae**

#### *Cydnini*

##### *Dallasiellus discrepans* (Uhler), 1877

Ovipositor facing caudad. Eighth paratergites (fig. 510) not fused medianly. An elongate narrow sclerite found dorsally lying between eighth paratergites, probably representing remains of the bridge between them. Tenth sternum divided; ninth paratergites small oblong lying on either side of fused second gonocoxae, latter clearly visible as a crescent shaped sclerite almost divided into two by a deep ventral cleft; bases of second gonapophyses visible. First gonocoxae large plate-like. Sclerotized rami present; ring sclerites present.

Spermatheca quite unlike any figured by Pendergrast (1957) for Cydnidae. Spermathecal duct broad becoming somewhat dilated distally and bearing internally a short stout sclerotized rod, a narrow duct passing down the centre of this rod and into a broader coiled duct, passing to pumping region (fig. 511) from dilation, pump with well developed proximal and distal flanges; spermathecal bulb pear shaped.

##### *Cyrtomenus crassus* (Walker), 1867

External genitalia (fig. 512) very similar to *Dallasiellus discrepans*; eighth paratergites joined medianly by a very narrow bridge; bases of second gonocoxae not visible externally. Sclerotized rami present; no ring sclerites.

Spermatheca differing somewhat from that of *Dallasiellus discrepans* although built along same lines. Spermathecal duct (fig. 513) basally

wide, narrow medianly, and distally expanding into a globular chamber within which is a second globular chamber, longitudinally ridged; a stout sclerotized duct originating from inner chamber and linking external chamber to pump; latter with well developed distal and proximal flanges; spermathecal bulb oval, attached directly to pump.

*Pangaeus aethiops* (Fabricius), 1787

External, internal genitalia, and spermatheca (fig. 514) similar to *Dallasiellus discrepans*. Internal rod of spermathecal diverticulum much less heavily sclerotized; spermathecal bulb globular.

*Amnestini*

*Amnestus pallidus* (Zimmer), 1910

External genitalia most unusual, described and figured by Froeschner (1960). Eighth paratergites (fig. 515) small V-shaped structures lying one on either side laterally. Greater part of external genitalia consisting of a large triangular sclerite surrounding an oval anal aperture, probably representing fused ninth paratergites and tenth sternum. First gonocoxae laterally placed, moveable, partly hidden by the margin of the seventh sternum.

Base of spermathecal duct narrow opening into a small mound or evagination of genital chamber; a small accessory spermathecal diverticulum (fig. 516) opening into base of spermathecal duct. Medianly spermathecal duct widening and thrown into two or three tight coils terminating in an oval spermathecal bulb. Pumping region not clearly evident although a small flange is present at base of spermathecal bulb.

*Amnestus pusio* (Stål), 1860

External, internal genitalia, and spermatheca (fig. 517) similar to *Amnestus pallidus*. Eighth paratergites not clearly delimited, spermathecal bulb spherical.

*Sehirini*

*Sehirus cinctus* (Palisot de Beauvois), 1805

Wagner (1963) gives a general description of the *Sehirus* type of genitalia using *Tritomegas sexmaculatus* Rambur as an example. Scudder (1959) gives a more complete general description for *Sehirinae*.

In *Sehirus cinctus*, eighth paratergites (fig. 518) continuous above the anus, external genitalia otherwise similar to *Tritomegas sexmaculatus*. Internally no sclerotized rami or ring sclerites present, differing in this respect from Scudder's general description for this group.

Spermatheca very similar to that of *Sehirus bicolor* (Linnaeus) figured by Pendergrast (1957). Basally spermatheca wide (fig. 519) and with numerous annulations apically narrowing and attached to a large spermathecal bulb; pumping region part of basal portion of spermathecal bulb, clearly marked by proximal and distal flanges.

## DISCUSSION

The female genitalia present a remarkably uniform picture throughout this superfamily. Scudder (1959) made a detailed study of the female genitalia of Heteroptera and Pendergrast (1957) of the spermathecae. Dupuis (1955) deals with the morphology of the genitalia in very general terms. Several other workers have dealt with various genera and families within the Pentatomoidea, their work has been incorporated where relevant.

**Pentatomidae - Scutellerinae***Odontoscelini*

The external genitalia are very uniform in this group. The spermathecal bulbs of the four species placed in this tribe tend to be elongate. One species, *Phimodera binotata*, possesses a spermathecal diverticulum and lacks the sclerotized canal running from the spermathecal entrance in the base of the genital chamber, found in the remaining three species. The female genitalia and spermathecae are very similar to those of the Pachycorini.

*Eurygastrini*

*Eurygaster alternatus* is well placed in a tribe of its own since it possesses sclerotized and interlocking rami, a character found only among members of the tribe Scutellerini so far. However, the spermatheca is much more similar to species in the Odontotarsini and Pachycorini because it lacks the sclerotized spermathecal dilation and heavily sclerotized spermathecal bulb of the Scutellerini.

*Pachycorini*

All species examined in this tribe possess a sclerotized groove or sclerite running along the genital chamber from the spermathecal entrance. The spermatheca itself varies somewhat. All but two species have either a spermathecal diverticulum or a dilation. The spermathecal diverticulum is membraneous and sac-like and is either attached mid-way to the spermathecal duct by means of a branch duct (*Stethaulax marmoratus*, fig. 441) or is entirely separate (*Acantholomidea porosa*, fig. 434). The spermathecal dilation is generally membraneous but is tough and sclerotized in *Diolcus irroratus* (fig. 424). *Chelysomidea guttata* is very unusual in possessing only one pair, (the outer) of sclerotized rami suggesting a relationship with the Scutellerini. However, its spermatheca is much more typical of the Pachycorini in possessing a weakly defined pumping region, and elongate sausage-like spermathecal bulb (fig. 438).

*Scutellerini*

*Augocoris gomesii* was the only North American species studied. Pendergrast (1957) studied five species of scutellerines. The spermatheca is characterized by the development in this group only of a very tough sclerotized globose spermathecal diverticulum and a well defined pumping region with proximal and distal flanges.



**Pentatomidae - Pentatominae***Pentatomini*

As pointed out in the introductory remarks, the genitalia and spermathecae of this subfamily are remarkably homogeneous. The presence or absence of spiracles on the eighth paratergites appears to be a random character of specific value only. However, in nine species a very distinct character was noted, the spermathecal bulb had a series of hollow horn-like projections varying in number from two to four. The significance of these structures is unknown. This character does not occur in any of the species possessing an elongate endophallic duct and hence does not reinforce in any way the division into two groups found among the males of the North American genera.

Other characters included ring sclerites, found otherwise in only two European species *Pentatoma rufipes* and *Eysarcoris aeneus*. It would be interesting to know if this was common to all palaearctic genera, however, little work has been done at this level on the palaearctic fauna. Scudder (1959) notes that ring sclerites may be present, also a tendency for the development of additional sclerotizations around the opening of the spermathecal duct. Most species examined in the present study possessed one or two small sclerites around the spermathecal opening.

*Thyanta perditor* was slightly unusual in possessing an elongate spermathecal bulb (fig. 479) with a peculiar pumping region but was otherwise normal. The most aberrant species examined was *Trichopepla semivittata* in which the spermatheca was a simple sac resembling that of the Cryptostemmatidae. However further work will have to be done on this genus to elucidate its homologies.

*Halyini, Edessini, Discocephalini, Sciocorini and Mecidiini*

Specimens examined from all these tribes all proved to have genitalia similar to those of the Pentatomini. *Brochymena* (Halyini) and *Edessa* (Edessini) have processes on the spermathecal bulb.

**Pentatomidae - Asopinae**

The female genitalia and spermathecae of species in this subfamily are very similar to those of the Pentatominae, a fact noted by Pendergrast (1957). The female genitalia and spermatheca show a remarkable uniformity throughout the group, paralleling that found in the male genitalia. Based on the female genitalia and spermatheca the Asopinae are very closely related to the Pentatominae.

**Pentatomidae - Podopinae**

Genitalia and spermatheca are similar to those of the Pentatominae and the spermathecal bulb has two to three processes. This subfamily, as in the case of the Asopinae, is very closely related to the Pentatominae on the basis of the spermatheca and female genitalia.

**Acanthosomidae**

The genitalia of the two species examined are like those of the Pentatominae externally; internally, sclerotized rami are present,

agreeing with Scudder's (1959) general description. The spermatheca has no diverticulum, differing in this respect from the general pentatomid type. *Acanthosoma haemorrhoidale* (Linnaeus) figured by Pendergrast (1957) also lacks a spermathecal diverticulum.

Unfortunately very few acanthosomids have been studied so far. A total of six species (in four genera) of the world's fauna have been described including the two species in this paper. On the basis of the female genitalia the Acanthosomidae appear to be distinct from the Pentatomidae in possessing sclerotized rami and in the form of the spermatheca. More work needs to be done on this family before a definitive statement can be made about its relationships. The status of this family is considered below.

#### **Tessaratomidae**

Pendergrast (1957) figures the spermatheca of four species of tessaratomids, Kumar (1962) describes and figures the genitalia of four species and the spermatheca of one; Scudder (1959) examined three species. Sclerotized and interlocking rami were found in *Piezosternum subulatum*, consistent with Scudder's description. Kumar (1962) noted that in two species of Oncomerini the rami were absent, but were present in *Stilidia* sp. The spermatheca of *Lyromorpha rosea* (Westwood) is very similar (Kumar 1962) to that found in the Pachycorini (Scutellerinae) as is the spermatheca of *Musgravea sulciventris* (Pendergrast 1957). The spermatheca of *Piezosternum subulatum* does not resemble that of *Musgravea* very greatly, consisting of a wide long spermathecal duct terminating in a pumping region and bulb (fig. 502). This tends to reinforce the observation made in the discussion of the male genitalia that the subfamily Oncomerinae is taxonomically heterogeneous. Other species described all show great similarity to one another (Pendergrast 1957). They have in common an ovoid spherical spermathecal dilation which is lacking in *Piezosternum*.

#### **Cydnidae**

The major works on Cydnidae (Froeschner 1960, Wagner 1963), deal only with the external female genitalia and these give very little clue to the relationships within this complex group. Scudder (1959) has examined the genitalia of nine species; Pendergrast (1957) has figured the spermatheca of four species; and Kumar (1962) the female genitalia of four species and the spermatheca of two. The present study deals with seven species, intended only to give a general idea of the relationships of the Cydnidae. However, such a diversity of form was discovered especially in the type of spermatheca, that much more work will have to be done to elucidate the systematics of this family. Some tentative ideas are presented, based on this and other work mentioned above.

#### **Cydnidae - Corimelaeninae**

Two species, *Corimelaena pulicaria* and *Galgupha nitiduloides*, were examined. The genitalia were similar in both species agreeing with the general description given by Scudder (1959). The spermathecae differ, however, quite radically. *Corimelaena pulicaria* has a simple spermathecal

duct with no diverticulum or dilation, terminating in a pump and spermathecal bulb, resembling very closely the spermatheca of acanthosomids and plataspids. *Galgupha nitiduloides* has a sclerotized groove extending from the entrance of the spermathecal duct in the genital chamber and a large sac-like spermathecal diverticulum resembling very closely the type of spermatheca found in the Pachycorini (Scutellerinae). An identical type of spermatheca was found in *Galgupha ovalis* by Pendergrast (1957). However *Thyrecoris scarabaeoides* (Pendergrast 1957) has a third type of spermatheca which is similar to the one found in several species of Cydnini (see below). This suggests that the subfamily Corimelaeninae is a composite grouping. Pendergrast (1957) states that further species should be examined to show whether *Galgupha ovalis* is aberrant in its type of spermatheca or whether there is diversity of form in this subfamily. There is indeed diversity of form and further work needs to be done in this group.

#### Cydnidae-Cydninae

##### *Cydnini*

Three species were examined and all showed marked similarities. The female genitalia are somewhat more complicated in *Dallasiellus discrepans*, two series of sclerites being found above the anus, the dorsal-most probably representing the median section of the eighth paratergites. Sclerotized rami are present in this group, these are not found in the Coremelaeninae. Ring sclerites were found in *Dallasiellus discrepans* and *Pangaeus aethiops*, although Scudder (1959) stated that these are absent.

The spermatheca is very similar in all forms possessing a small spermathecal dilation within which is a stout sclerotized rod, globular in *Cyrtomenus crassus*. The same type of spermatheca was found in the species studied by Pendergrast (1957) and in *Stibaropus callidus* (Kumar 1962). The latter author however found a completely different type of spermatheca in *Geotomus apicalis*. In this species the spermathecal duct is very long and highly coiled and the dilation is lacking. Pendergrast (1957) notes the similarity of the type of spermatheca with a dilation and internal rod to that found in the Pentatomidae. The cydnid dilation is, however, much modified, the whole structure being smaller and stouter than the structure found in the Pentatominae. Wagner (1963) has created a new tribe Geotomini and this division may be further confirmed on the basis of the spermatheca.

##### *Amnestini*

Two species were examined and these showed a highly aberrant type of genitalia and spermathecae. Froeschner (1960) describes the peculiar triangular plate which surrounds the anal opening. Its exact homology is difficult to determine but probably represents the fused ninth paratergites and tenth sternum. The spermatheca is unique, consisting of a wide highly coiled spermathecal duct terminating in a spermathecal bulb, no pumping region was apparent. Adjacent to the spermathecal opening into the vulva is a small sac-like diverticulum.

It would appear that on the basis of the female genitalia and



spermatheca, the Amnestini probably deserve at least subfamily status.

#### *Sehirini*

The genitalia of *Sehirus cinctus* do not resemble those of *Sehirus bicolor* figured by Scudder (1959). Contrary to his general description of this group, sclerotized rami and ring sclerites were not found in *Sehirus cinctus*. The spermatheca of *S. bicolor*, (Pendergrast 1957) is not the same as that of *S. cinctus*, the latter species possesses a basal dilation connected by a short duct to the pump and bulb (fig. 519). The dilation does not appear to have the sclerotized rod found in the Cydnini. The position of *Sehirus cinctus* is doubtful and is discussed below.

### INTERRELATIONSHIPS AND CLASSIFICATION OF THE PENTATOMOIDEA

A great deal of work has been done on the systematics of the Heteroptera of which the Pentatomoidea are a part. However, I feel that too much emphasis has been laid on results obtained from a very small number of species examined in the various families. It became clear after detailed examination of the North American Pentatomoidea that great variation of structure occurs in all families and that workers choosing but a few random species would get and have got quite an erroneous impression of the group as a whole. This is particularly so among the male genitalia of the Scutellerinae where the only work previously done was by Leston (1952) on the tribe Pachycorini. The results proved to be quite startlingly different from those obtained by other workers examining species only from the Scutellerini.

Pruthi (1925), Pendergrast (1957), Scudder (1959), Leston (1958), Manna (1958), and Miyamoto (1961), have dealt with the classification of the Pentatomoidea from various points of view. Leston *et al.* (1954) proposed a classification of terrestrial Heteroptera based on a synthesis of all previous morphological work on this group. Its weakness, as China (1955) points out, is in the fact that most of the previous work on the Heteroptera had been rather fragmentary and dealt with rather small samples in the various groups each worker had had under consideration. The present work will help fill in some gaps in our knowledge, but it cannot be regarded as being complete in any way and any conclusions reached must be regarded with some reserve.

I shall consider first the phylogeny and relationships of the Pentatomoidea. This superfamily together with the Pyrrhocoroidea, Lygaeoidea, Coreoidea, Piesmatoidea and Aradoidea forms the group Pentatomorpha (Leston *et al.* 1954). The following features are characteristic for the Pentatomoidea. The males have the ninth segment developed in the pygophore in which are found a pair of claspers and the aedoeagus. The latter consists of a toughened theca, the conjunctiva which generally bears one to three pairs of conjunctival appendages and the vesica. The seminal duct generally enters a sclerotized ejaculatory reservoir, variously modified, and this in turn connects with the endophallic duct, which opens at the secondary gonopore. The female genitalia

are of the plate-like type (Scudder 1959). Ring sclerites and rami may be present. The spermatheca is characterized by a well marked pumping region, generally with proximal and distal flanges, terminating in a spermathecal bulb of varied shape.

The Coreoidea and Pyrrhocoridea are, on the basis of the female genitalia, the closest to the Pentatomoidea in possessing a plate-like ovipositor (Schaefer 1964). The Lygaeoidea, on the other hand, have a lacinate type of ovipositor, with some exceptions. The male genitalia of the coreoid complex are probably the closest to the pentatomoid type in possessing a distinct ejaculatory reservoir and membranous conjunctival appendages (Scudder 1957), but the vesica is different in that the endophallic duct in the coreoids is generally very elongate (Pruthi 1925, Scudder 1957). *Piezosternum* (Tessaratomidae) has, however, a very highly endophallic duct within the apex of the vesica and if this were extrusible it would produce a very long apical duct. The latter would resemble the very long coiled endophallic ducts found in the Lygaeidae (Ashlock 1957). The remainder of the families in the Pentatomoidea have a relatively short vesica with exception of a few genera in the Pentatominae. The latter group is probably a highly specialized development of the normal pentatomine type.

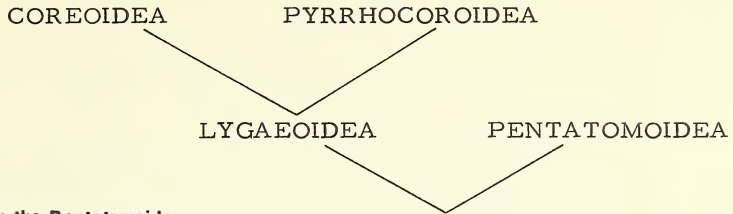
Miyamoto (1964) found that the coreoids showed resemblances to the pentatomoids on the basis of the gastric caeca but that the structure of the salivary gland resembled that of the pyrrhocorids.

The cytogenetics of the pentatomoid group is complex and evidence for relationship with other groups is not clear cut. Leston (1958) found two distinct groups within the Pentatomoidea: the Acanthosomidae, Tessaratomidae and Scutelleridae with  $2n = 12$  chromosomes, and the Pentatomidae with  $2n = 14$ . However, in the latter family chromosome numbers range from  $2n = 6$  to  $2n = 27$ . Neither the Coreoidea nor the Lygaeoidea show close relationship to the Pentatomoidea cytologically. The coreoids have varying chromosome numbers with a mode of  $2n = 21$ . The Lygaeidae on the other hand have also variable chromosome numbers but have a diploid number of  $2n = 14$ . The coreoids have an XO sex mechanism, the lygaeids an XY sex mechanism resembling the Pentatomidae. However, the latter family does not possess m-chromosomes found in a great majority of the species of lygaeids.

Manna (1958) derives the Lygaeidae from the Pentatomidae on the basis of cytological evidence. This I doubt on the basis of evidence from the male and female genitalia, the lygaeids generally possessing a primitive lacinate type ovipositor.

Schaefer (1964), on the basis of a vast amount of data, derived both the Coreoidea and Pyrrhocoroidea from the Lygaeoidea. The Pentatomoidea show some relationship to the above superfamilies but this is not very close. The Pentatomoidea probably were derived independently of the lygaeoids from some common ancestor, as suggested by China's (1955) diagram of the relationships of the heteropterous families. Leston (1958) and China and Miller (1959), on the other hand proposed independent origins for the Lygaeoidea, Coreoidea and Pentatomoidea from a common ancestor. The evidence obtained so far indicates that the latter theory is closer to reality.

The relationship of the four groups is shown below.



#### Relationships within the Pentatomoidea

##### *Ranking of the Scutellerinae*

The status of the Scutellerinae has posed quite a problem in the past. Now that all representative tribes have been examined, I am inclined to agree with Pendergrast (1957) and Kumar (1962), and raise the Scutellerinae to family rank. The group is, however, difficult to define on the basis of the male and female genitalia. The Scutellerini form a distinct group possessing in the males three pairs of conjunctival appendages, with the third generally heavily sclerotized and S-shaped. The vesica has a long convoluted duct and the endophallic duct is short. The females have paired sclerotized rami and the spermatheca has a heavily sclerotized dilation and a distinct pumping region. The Eurygastrini show characters intermediate between the Scutellerini and Pachycorini. They have sclerotized and interlocking rami in the females. The spermatheca is, however, much simpler, lacks a dilation and flanges in the pumping region but there is a sclerotized groove in the genital chamber running from the spermathecal opening, a characteristic of the Pachycorini.

The genus *Eurygaster* has been raised to tribal status by Lattin (1964) and this is supported by my own work. However, Wagner (1963) raised this group to family level, and this I think is hardly warranted on the basis of the morphology of the genitalia. The tribe shows very great similarities to the other tribes within the Scutellerinae, especially the Pachycorini. The latter tribe and the Odontotarsini are very similar. Both groups possess elongate sclerotized grooves in the floor of the genital chamber, a feature not found in the Pentatominae. Rami are lacking except in one species *Chelysomidea guttata* (Pachycorini) in which only the outer rami are present. The spermatheca has either a simple duct or a membranous diverticulum attached half way along the spermathecal duct, or separately at the base of the duct (sclerotized in *Diolcus irroratus*). All these types of spermatheca do not resemble in any way the elongate dilation with central rod found in the Pentatominae. More work will have to be done on the Palaearctic species of the Odontoscelini before an adequate definition of this tribe can be made.

##### *Relationships within the Pentatomoidea*

The Pentatominae and Podopinae are remarkably constant in genitalic characters. The male and female genitalia of the Asopinae show remarkable similarity to one another and to the Pentatominae. I think on this basis the subfamily should be downgraded and given tribal status



within the Pentatominae. The characters possessed in common by all genera in the Asopinae such as the genital plates and thecal shield are also found in species of the Pentatominae but never in combination. The internal structure of the vesica is typically pentatomine and the structure of the spermatheca is identical to that found in that subfamily. The similarity of the Asopinae to the Pentatominae was noted by Leston (1954a).

The Podopinae and Asopinae are very closely related. The Podopinae lack genital plates but have in their place a pair of pygophoral appendages. The structure of the aedoeagus and vesica is identical in both subfamilies. Leston (1953a) raised the podopines to subfamily status but felt that further research might lead to a drop in its rank. On the basis of the work done by Barber and Sailer (1953) and the present study this group should be given tribal status within the subfamily Pentatominae. Pendergrast (1957) states that the Podopinae and Asopinae are so close to the Pentatominae that they should either be lowered in status or that the other subfamilies should be raised in status. I think the former course more desirable because of the very close affinities this group shows to the Pentatominae.

#### *Tribal status in the Pentatominae*

Within the Pentatominae the tribes Halyini and Mecidiini on the basis of the male and female genitalia are so similar to the Pentatomini that these two tribes should be given subtribal status or incorporated into the Pentatomini as genera. However, other genera within the Halyini may warrant tribal status. The vesicae of five species of Australian Halyini have been described by Kumar (1964) and these all resemble the typical plan found among Pentatomini. Ruckes (1946, 1958) who has made a major study of this group, has not described the internal details of the male genitalia. The genitalia of the Mecidiini studied by Sailer (1952) were all remarkably uniform in character and are similar to the Pentatominae.

The Discocephalini have recently been raised to subfamily status by Ruckes (1960, 1963). However, I hesitate to follow such a step until further work has been done on the male and female genitalia of the species in this tribe. Ruckes (personal communication) informs me that he has several excellent characters which distinguish this tribe from others in the Pentatominae. The male genitalia of *Lineostethus clypeatus* differ but slightly from the pentatomid type in having a thickened sclerotized ring at the base of the endophallic duct. The female genitalia are typically pentatomine in construction.

A single species of both the Edessini and Sciocorini was studied. In both the female genitalia were typically pentatomine. The male genitalia, however, showed slight differences from the general pattern especially in *Edessa bifida*. More work will have to be done on these groups before any definitive statement can be made. It would seem, however, that both these tribes are fairly closely related to the Pentatomini.

*Status of the Acanthosomidae*

The Acanthosomidae have been accorded family status by Leston (1953b). China (1959) retains the group as a subfamily of the Pentatomidae. On the basis of the male genitalia I agree with China. The acanthosomids are undoubtedly older and less specialized than the pentatomines in many respects. The spermatheca lacks the highly specialized dilation it has in the pentatomines. Leston (1958) found the chromosome number to be  $2n = 12$  with an XY sex determining mechanism, characters common to the Scutellerinae. Both Dupuis (1948) and Southwood (1956) consider the Acanthosomidae to be a primitive family.

*The Cydnidae*

A preliminary study of a few species in this family has revealed a considerable diversity in the structure of the genitalia and the family is one of great interest. Froeschner (1960) was dubious regarding the phylogenetic relationships indicated by the presence of a fringe of close set bristles on the apices of the middle and posterior coxae, external morphological characters used to distinguish members of this family from other families in the Pentatomoidea. He goes on to question the value of characters used to define groups within the Pentatomoidea as indicators of phylogeny within this superfamily as a whole. From a study of the male and female genitalia it becomes clear that the Cydnidae is a somewhat heterogeneous assemblage. This view was also held by Pendergrast (1957).

Very little can be said regarding the Corimelaeninae at this stage. The male genitalia of *Corimelaena pulicaria* do not resemble the general pattern found in the Pentatominae, as three pairs of conjunctival appendages were found, and the theca possessed a peculiar pair of thecal appendages; the vesica is simple. The male genitalia of species figured by McAtee and Malloch (1933) appear to resemble *Corimelaena pulicaria* in many details. The two spermathecae examined were quite different; one was similar to the acanthosomid type and the other to the pachycorine (Scutellerinae). The genitalia show very little similarity to those of the Cydninae studied so far. It may be that on further investigation the present recognition of Corimelaeninae as a family by specialists in North America will achieve wider acceptance.

The Cydninae, on the basis of male and female genitalia so far examined show relationship with the Pentatominae. The eggs (Southwood, 1956) show similarity to those of the Pyrrhocoridae and some Lygaeidae. Southwood (1956) stated that the family as a whole was rather ancient and closer to the Tessaratomidae than to the Pentatomidae. The ovariole number (Miyamoto 1957, Woodward 1950) for the majority of species examined was seven which is also the most frequent number found among Pentatominae. Little work has been done on the chromosomes of this subfamily (Leston 1958, Manna 1958).

The relationships of the Cydnidae will not be discussed further. I feel at the moment that too little is known about the basic morphology of the species in this family and further research needs to be done.

*Phylogenetic considerations*

The ancestral pentatomoid probably had very simple male genitalia. The vesica was long, the seminal duct probably entered into a simple sac-like ejaculatory reservoir. Conjunctival appendages, if present, were small and membranous. The female spermatheca was a simple duct terminating in a pumping region and spermathecal bulb. The ovipositor was of the plate-shaped type. The Tessaratomidae are probably the most primitive family (Leston 1954d) with *Piezosternum* being the most primitive genus so far examined in the family. *Piezosternum* both in the structure of the aedoeagus and spermatheca shows definite coreoid affinities and is radically different from other members of this family, e.g. *Musgravea sulciventris*. *Piezosternum* is probably very close to the ancestral pentatomoid which gave rise to the variously modified groups in this superfamily.

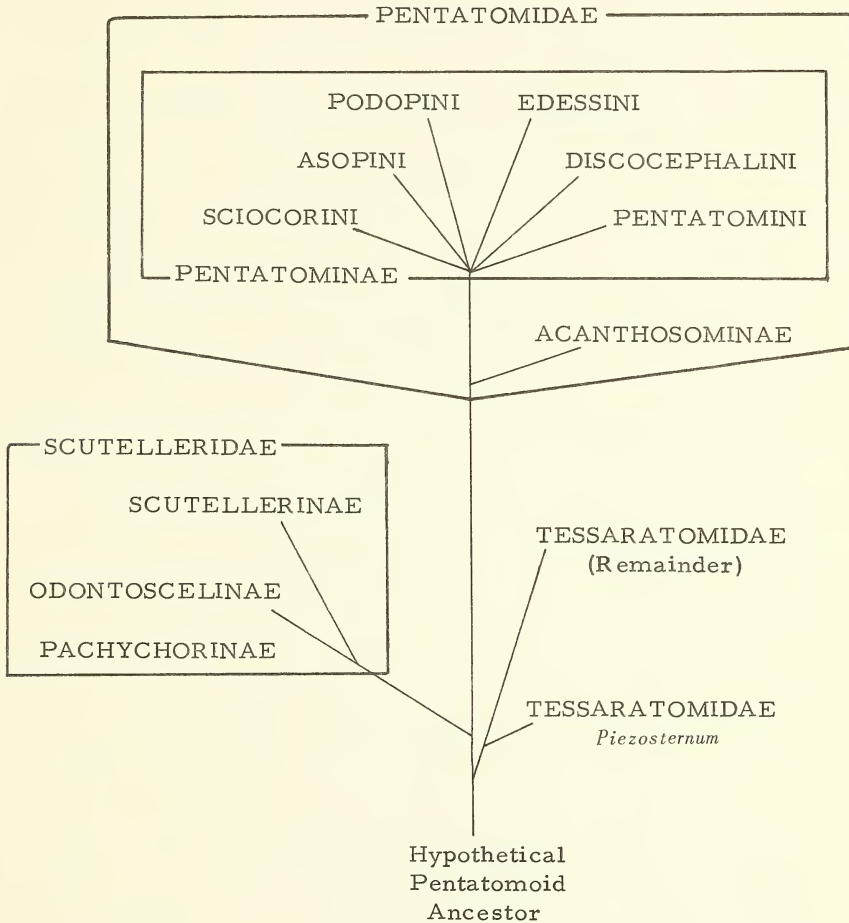
The ancestral pentatomoid stock appears to have evolved into two distinct lines, the Scutelleridae and the Pentatomidae. In the Scutelleridae the male genitalia became slightly more complex with the seminal duct opening into an internal canal within the ejaculatory reservoir. Conjunctival appendages became more complex but were still generally membranous. The spermatheca was still simple but in some cases possessed a diverticulum or dilation. These characters are typical of Pachycorinae and Odontoscelinae. The Scutellerinae are the most highly evolved and specialized group. The third conjunctival appendages have become sclerotized and S-shaped. The vesica has a specialized convoluted duct and the endophallic duct has become very much shortened. The females possess interlocking and sclerotized rami, a distinctly non-pentatomine character, and the spermathecal duct has a sclerotized dilation.

Within the Pentatomidae, the Acanthosominae must be considered a very early offshoot of the pentatomid stock but still closely related to the Pentatominae. The females retain the simple type of spermatheca but have developed sclerotized rami in the ovipositor, parallelling the Scutellerinae. The male genitalia, in the structure of the vesica, resemble the Pentatominae closely in that the seminal duct either opens into an internal canal within the ejaculatory reservoir, or directly into the reservoir. The conjunctival appendages tend to be more specialized and are sclerotized. As pointed out previously the Acanthosominae retain the more primitive chromosome number  $2n = 12$  (Leston 1958) and very likely represent an early group in the development of the more highly specialized Pentatominae.

The Pentatominae have generally retained a simple vesica with the seminal duct opening into the ejaculatory reservoir via an internal canal. The North American fauna have evolved a small group of very specialized species in which the endophallic duct has become enormously lengthened and coiled; the ejaculatory reservoir has a complex series of internal ducts. The Pentatominae have developed two specialized features, the sclerotized median penial lobes and the dilation with internal rod of the spermatheca. Sclerotized rami have not been developed in this group. The type of spermatheca is quite constant throughout this subfamily with the sole exception of *Trichopepla semivittata* in which the



spermatheca is sac-like. The median penal lobes are not found in all species. The Asopini, Podopini, Edessini, Discocephalini and Sciocorini are all very recent specializations of the main pentatominae stock and retain many characters in common with the latter group. The phylogenetic sequence of the Pentatomoidea excluding the Cydnidae follows:



The paired sclerotized rami found in the female genitalia have apparently evolved independently three times, in the Tessaratomidae (*Piezosternum*), the Scutellerinae, and the Acanthosominae. Spermathecal dilations have evolved twice. The Pentatominae have developed the specialized membraneous dilation with internal rod and the Scutellerinae a heavily sclerotized and less specialized dilation. In the male genitalia specialized structures have evolved in great profusion in each group. Median penal lobes have apparently evolved in two groups, the Pentatominae and in the Scutelleridae where they are found in a single species *Symphylus caribeanus*. The conjunctival appendages are subject to great change and have become variously modified in each subfamily.

**Proposed Classification of Families, Subfamilies and Tribes of North American Pentatomoidea**

SCUTELLERIDAE

Odontoscelinae  
Eurygastrinae  
Pachycorinae  
Scutellerinae

PENTATOMIDAE

Pentatominae  
Pentatomini  
Edessini  
Discocephalini  
Sciocorini  
Asopini  
Podopini  
Acanthosominae

CYDNIDAE

Corimelaeninae  
Cydninae  
Cydnini  
Amnestini  
Sehirini

TESSARATOMIDAE

Piezosterninae

KEY TO GENERA OF NORTH AMERICAN SCUTELLERIDAE  
BASED ON MALE GENITALIA

1. Vesica with long convoluted duct, extending from anterior end into ejaculatory reservoir (fig. 30) . . . . . 2  
Vesica without such duct . . . . . 4
2. Endophallic duct with a broad oblong dorsal sheath (fig. 30); conjunctival appendages membranous . . . . . *Camirus* Stål 1862  
Endophallic duct without sheath; at least one pair of conjunctival appendages heavily sclerotized apically . . . . . 3
3. Ejaculatory reservoir globose (fig. 61); apex of vesica flattened . . . . . *Stethaulax* Bergroth 1891  
Ejaculatory reservoir elongate (fig. 83); apex of vesica tubular . . . . . *Augocoris* Burmeister 1835
4. Three pairs of sclerotized horn-like conjunctival appendages; theca with cylindrical ventral process (fig. 25) . . . . . *Eurygaster* Laporte 1832  
Never with all characters above . . . . . 5
5. Ejaculatory reservoir simple, sac-like composed of a single chamber, or absent . . . . . 6  
Ejaculatory reservoir complex; if apparently simple, large spiny third conjunctival appendages present (fig. 11) or apex of vesica with spiny processes one on either side (fig. 17) . . . . . 11
6. Ejaculatory reservoir absent; seminal duct opening directly into endophallic duct (fig. 36) . . . . . 7  
Ejaculatory reservoir present as a small diverticulum (fig. 56) . . . . . 8
7. Pygophore with dorsal margin produced into an elongate process (fig. 32); endophallic duct very short, not projecting beyond margin of theca . . . . . *Pachycoris* Burmeister 1835  
Pygophore with smooth dorsal margin; vesica with complex pumping apparatus (fig. 72); endophallic duct projecting well beyond margin of theca . . . . . *Diolcus* Mayr 1864
8. Apex of vesica covered with a number of stout spines and with a stout spiny dorsal process (fig. 55) . . . . . *Sphyrocoris* Mayr 1864  
Vesica without spines . . . . . 9
9. Three pairs of conjunctival appendages present, third spiny; apex of vesica very broad, covered with spines, basally with a number of partitions giving a coiled appearance (fig. 46) . . . . .  
. . . . . *Homaemus* Dallas 1851  
Only two pairs of conjunctival appendages present . . . . . 10
10. Dorsal margin of proctiger produced into a number of spiny processes (fig. 37); apex of vesica membranous . . . . . *Chelysomidea* Lattin 1965  
Dorsal margin of pygophore smoothly arched; apex of vesica sclerotized . . . . . *Tetyra* Fabricius 1803
11. Third conjunctival appendages present, broad and spiny (fig. 11) . . . . . 12  
. . . . .  
Third conjunctival appendages absent . . . . . 13
12. Second conjunctival appendages bifid, bearing two sclerotized horns (fig. 6) . . . . . *Fokkeria* Schouteden 1904  
Second conjunctival appendages bearing a large single horn . . . . .  
. . . . . *Euptychodera* Bergroth 1908



13. Vesica with a pair of spiny lobes, one on each side near apex (fig. 17) . . . . . *Vanduzeeina* Schouteden 1904  
Vesica without such lobes . . . . . 14
14. Endophallic duct basally with a very short convoluted section (fig. 22); only one pair of membraneous conjunctival appendages present. . . . . *Phimodera* Germar 1839  
Endophallic duct without convolutions; two pairs of conjunctival appendages present . . . . . 15
15. Apex of vesica very short projecting slightly beyond margin of theca (fig. 77); claspers broadly hook-shaped . . *Acantholomidea* Sailer 1945  
Apex of vesica long enclosed between median penal lobes (fig. 65); claspers T-shaped . . . . . *Symphylus* Dallas 1851

KEY TO GENERA OF NORTH AMERICAN PENTATOMINI  
BASED ON MALE GENITALIA

1. Endophallic duct very long, coiled (fig. 236), dorsal margin of theca with thecal processes (fig. 234), ejaculatory reservoir complex (fig. 236) . . . . . 2  
Endophallic duct short, theca with or without dorsal processes; ejaculatory reservoir generally simple with posterior canal (fig. 89) . . . . . 6
2. Ejaculatory reservoir moderately sclerotized, not possessing a number of lateral striae (fig. 250) . . . . . *Euschistus* Dallas 1851  
Ejaculatory reservoir very heavily sclerotized with a number of well marked striae laterally . . . . . 3
3. Two distinct pairs of membraneous conjunctival appendages, second with five lobes (fig. 233) . . . . . *Meneclis* Stål 1867  
One pair of conjunctival appendages generally only, shallowly divided . . . . . 4
4. Thecal processes with a distinct projection between them from margin of theca, conjunctival appendages elongate distinctly bifid (fig. 239) . . . . . *Coenus* Dallas 1851  
Combination of characters not as above, conjunctival appendages if bifid, broadly so . . . . . 5
5. Ventral border of pygophore with a deep median U-shaped emargination (fig. 241) conjunctival appendages broad, undivided (fig. 243) . . . . . *Hymenarcys* Amyot and Serville 1843  
Ventral border without emargination, conjunctival appendages broadly bifid (fig. 253) . . . . . *Prionosoma* Uhler 1863
6. Conjunctival appendages absent . . . . . 7  
Conjunctival appendages present . . . . . 8
7. Theca shield-like, enclosing a further sheath-like structure (fig. 228), claspers very complex (fig. 226) . . . . .  
. . . . . *Loxa* Amyot and Serville 1843  
Theca not as above, claspers trilobed (fig. 146) . . . . .  
. . . . . *Chlorocoris* Spinola 1837
8. Thecal shield present (fig. 183) . . . . . 9  
Thecal shield absent . . . . . 11

9. Seminal duct extended into dorsal canal, ejaculatory reservoir simple . . . . . 10  
Seminal duct extended into base of endophallic duct; ejaculatory reservoir divided (fig. 185) . . . . . *Murgantia* Stål 1862
10. Apex of vesica projecting well beyond the margins of the median penal lobes, not enclosed by them (fig. 108) . . . . .  
 . . . . . *Peribalus* Mulsant and Rey 1866  
Apex of vesica not or only slightly projecting beyond margins of median penal lobes which otherwise enclose apex . . . . . 11
11. Conjunctival lobe present, very large (fig. 179): ventral surface of pygophore vertical (fig. 177) . . . . . *Neotiglossa* Kirby 1837  
Conjunctival lobe small (fig. 131): ventral surface of pygophore horizontal . . . . . *Aelia* Fabricius 1803
12. Genital plates present . . . . . 13  
Genital plates absent . . . . . 14
13. Ejaculatory reservoir simple, with posterior canal; vesica S-shaped (fig. 154) . . . . . *Carpocoris* Kolenati 1846  
Ejaculatory reservoir with internal duct, vesica short . . . . .  
 . . . . . *Dendrocoris* Bergroth 1891
14. Median penal lobes absent . . . . . 15  
Median penal lobes present (fig. 170) . . . . . 18
15. Ejaculatory reservoir without posterior canal (fig. 114) . . . . .  
 . . . . . *Trichopepla* Stål 1867  
Ejaculatory reservoir with posterior canal (fig. 123) . . . . . 16
16. Conjunctival appendages divided into three distinct broad lobes (fig. 122). Endophallic duct short, curved (fig. 123) . . . . .  
 . . . . . *Brepholoxa* Van Duzee 1904  
Conjunctival appendages elongate; endophallic duct S-shaped (fig. 196) . . . . . 17
17. Theca with a small pair of projections one on each side, near base (fig. 199). Second conjunctival appendages present . . . . .  
 . . . . . *Cosmopepla* Stål 1867  
Theca without projections; second conjunctival appendage absent (fig. 194) . . . . . *Eysarcoris* Hahn 1834
18. Ejaculatory reservoir divided into two ducts by means of an internal septum . . . . . 19  
Ejaculatory reservoir simple, with posterior canal (fig. 128) . . . . . 20
19. Claspers flattened, leaf-like; lateral borders of pygophoral opening smooth . . . . . *Padaeus* Stål 1862  
Claspers, stout, wide, apically produced into cylindrical processes (fig. 175); lateral borders of pygophoral opening with a small oblong process, one on each side (fig. 173) . . . . . *Proxys* Spinola 1837
20. Ventral margin of pygophore flattened with two longitudinal ridges medianly (fig. 124) . . . . . *Arvelius* Spinola 1837  
Ventral margin without ridges . . . . . 21
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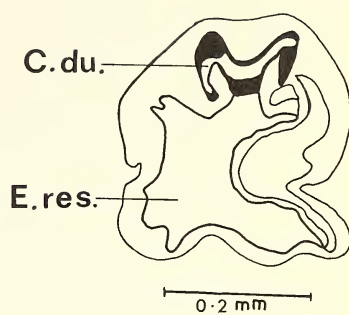
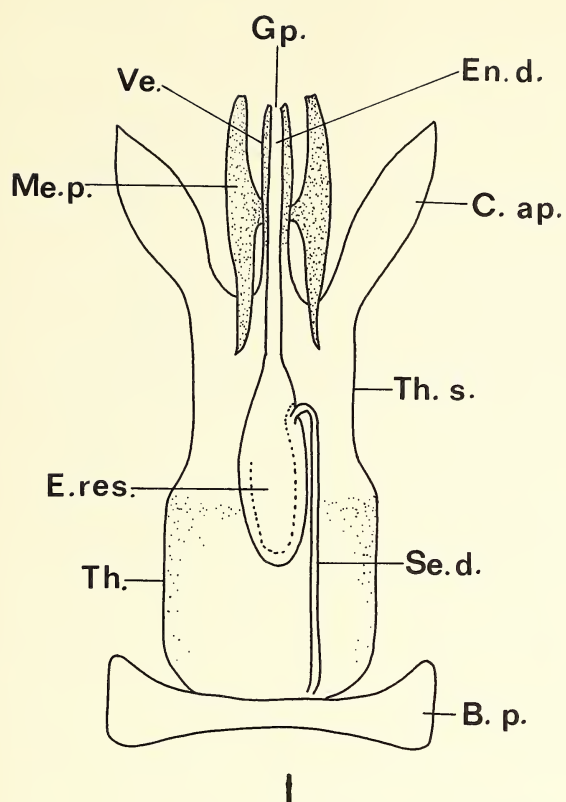
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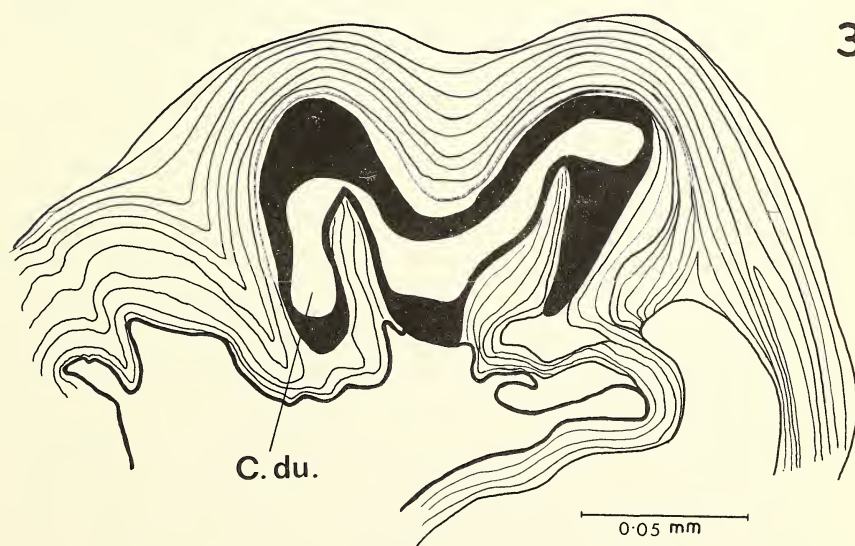
- A. ch., anterior chamber of ejaculatory reservoir  
 A. s., anterior sinus  
 A. th. pr., anterior thecal process  
 Ap., apodeme  
 Ar. cl., arm of clasper  
 B. p., basal plate  
 C. ap., conjunctival appendage  
 1 C. ap., first conjunctival appendage  
 2 C. ap., second conjunctival appendage  
 3 C. ap., third conjunctival appendage  
 C. ap.2, branch of second conjunctival appendage  
 C. du., convoluted duct  
 C. lo., conjunctival lobe  
 Ca., canal  
 Cal., callus  
 Ce. s., central sinus  
 Cl., clasper  
 D. b., dorsal border of pygophore  
 D. dv., dorsal diverticulum of theca  
 D. c. ap., dorsal lobe of conjunctival appendage  
 D. c. lo., dorsal conjunctival lobe  
 D. ch., dorsal chamber of ejaculatory reservoir  
 D. m., dorsal margin of pygophore  
 D. pr., dorsal process of vesica  
 D. r., dorsal reservoir  
 Du., duct  
 E. res., ejaculatory reservoir  
 En. d., endophallic duct  
 En. f., flange of endophallic duct  
 F., flange around pygophoral opening  
 G. pl., genital plate  
 Gp., secondary gonopore  
 In. r., inferior ridge  
 Kn., knob  
 L. a., lower arm of clasper  
 M. pr., median process  
 Me. p., median penal lobe  
 Mu., muscle fibre  
 P., proctiger  
 P. ch., posterior chamber of ejaculatory reservoir  
 P. th. pr., posterior thecal process  
 Pi., pit  
 Pr., projection  
 Pro., process  
 Py. ap., pygophoral appendage  
 R., sclerotized ring at base of endophallic duct  
 Ri., ridge  
 S. ve. pr., supra vesical process  
 Se., septum  
 Se. d., seminal duct  
 Sh., sheath of vesica  
 Si., sinus  
 Sp., spine  
 St., setae  
 Su. r., superior ridge  
 Th., theca  
 Th. ap., thecal appendage  
 Th. f., thecal flange  
 Th. pr., thecal process  
 Th. s., thecal shield  
 U. a., upper arm of clasper  
 V. b., ventral border of pygophore  
 V. c. ap., ventral lobe of conjunctival appendage  
 V. c. lo., ventral conjunctival lobe  
 V. ch., ventral chamber of ejaculatory reservoir  
 V. m., ventral margin of pygophore  
 Va., valve  
 Ve., vesica  
 Ve. f., vesical flange  
 Ve. pr., vesical process

**Figures 411-519 (female genitalia)**

- |   |   |
|---|---|
| A. s., accessory sac                                | O., opening of spermathecal duct into genital chamber |
| An., anal opening                                   | O. r., outer rami                                     |
| B., spermathecal bulb                               | P., spermathecal pump                                 |
| B. d., bulb of spermathecal duct                    | P. f., proximal flange of pump                        |
| D. f., distal flange of pump                        | Pch., pouch in genital chamber                        |
| Dl., dilation of spermathecal duct                  | Pr., process of spermathecal bulb                     |
| Dl. 1, proximal chamber of spermathecal dilation    | Pt. 8, paratergite eight                              |
| Dl. 2, distal chamber of spermathecal dilation      | Pt. 9, paratergite nine                               |
| Dt., diverticulum                                   | R., sclerotized rod                                   |
| Fl., flange   | R. sc., ring sclerite                                 |
| Gr., sclerotized groove in floor of genital chamber | S. 10, sternum ten                                    |
| 1 Gp., first gonapophysis                           | S. du., spermathecal duct                             |
| 2 Gp., second gonapophysis                          | Sc., sclerite   |
| 1 Gx., first gonocoxa                               | T. 8, tergum eight                                    |
| 2 Gx., second gonocoxa                              | Tr., triangulum                                       |
| I. r., inner ramus                                  |   |

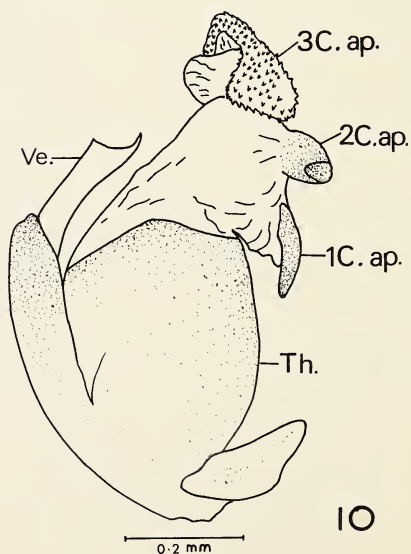
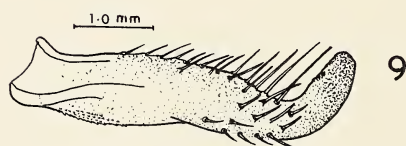
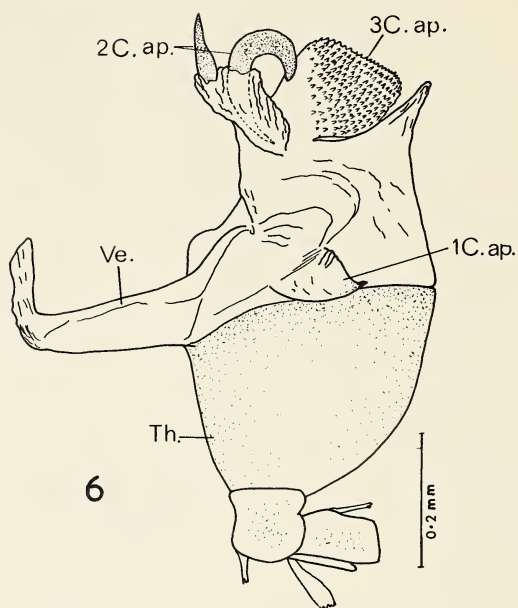
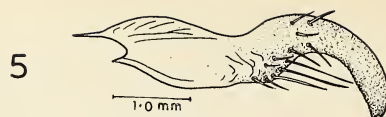
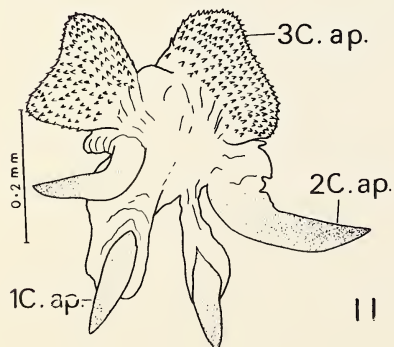
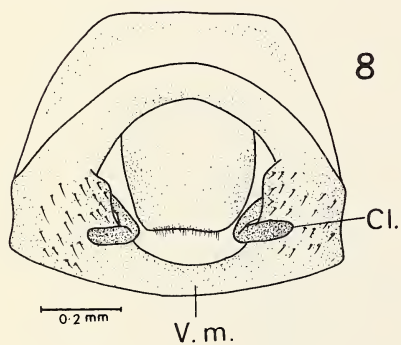
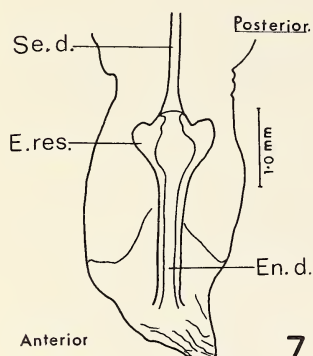
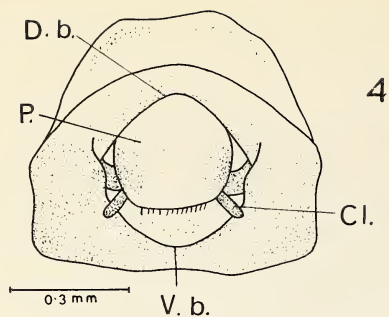


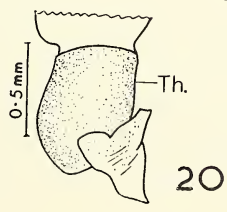
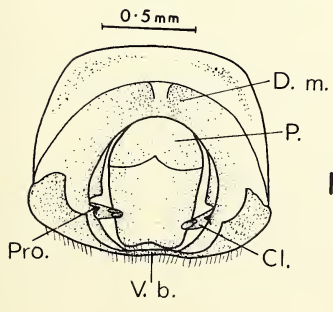
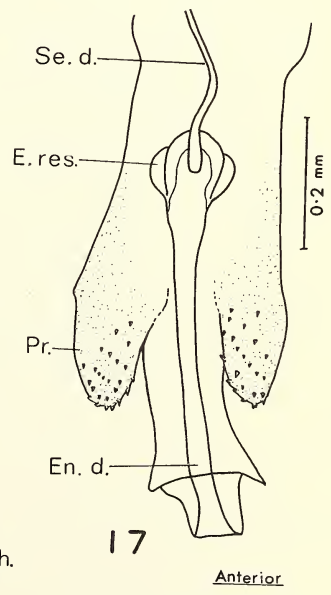
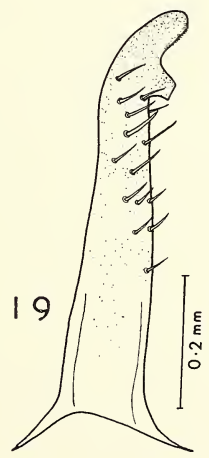
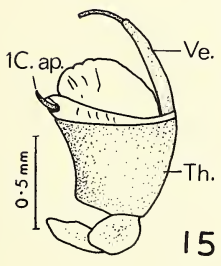
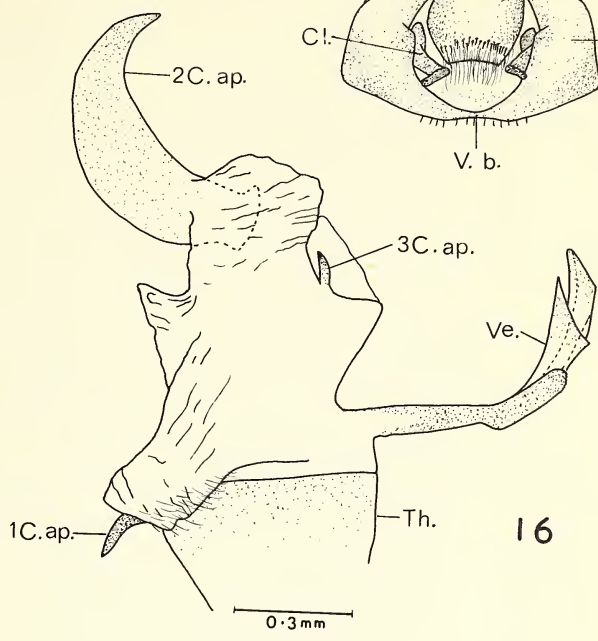
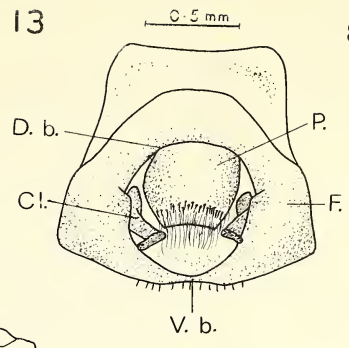
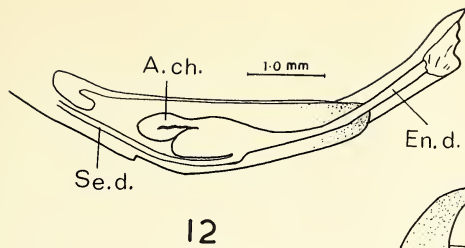
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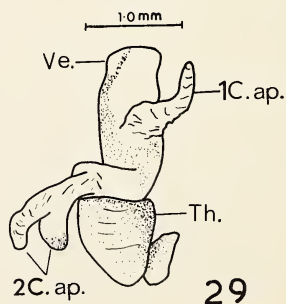
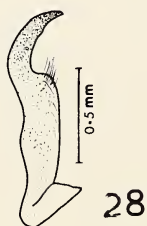
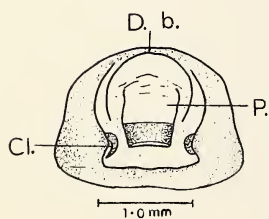
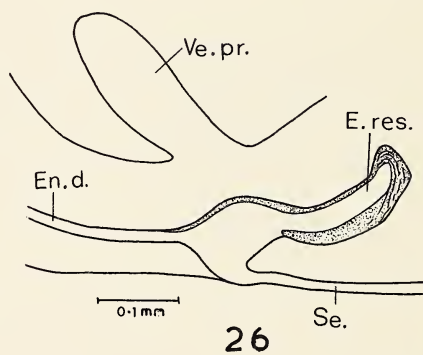
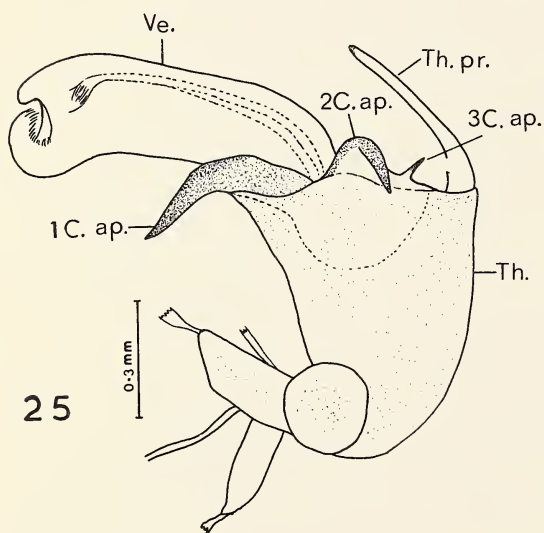
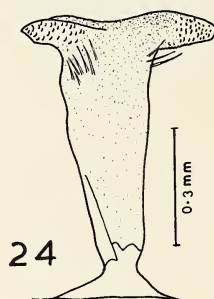
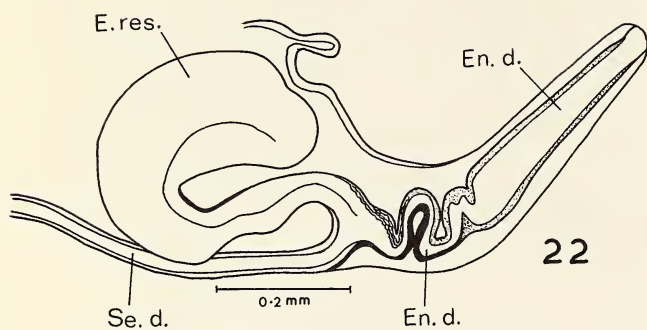
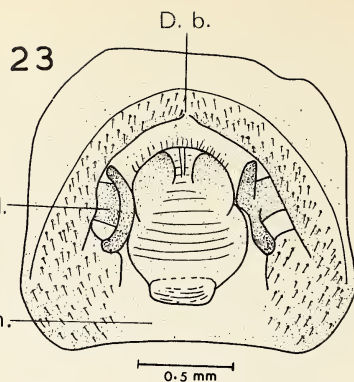
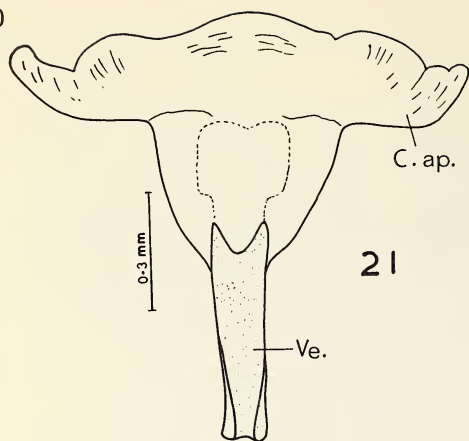
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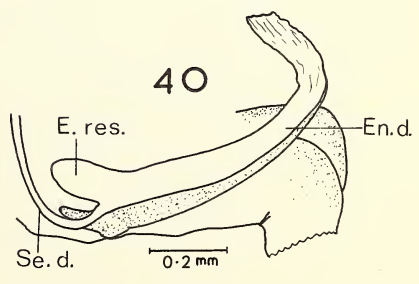
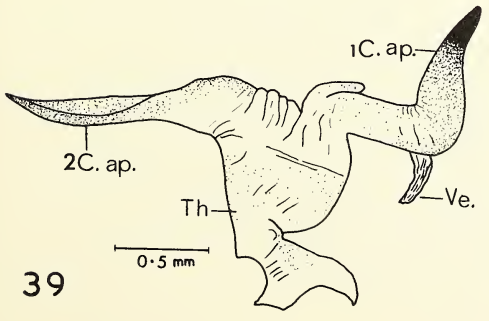
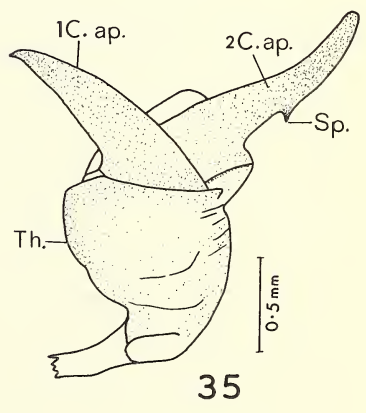
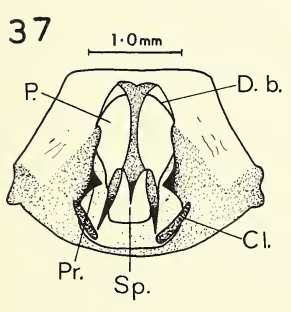
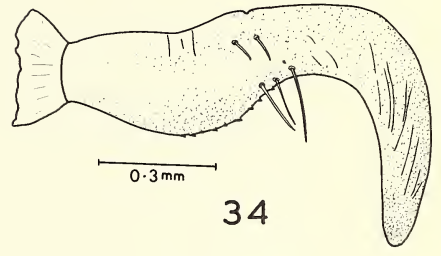
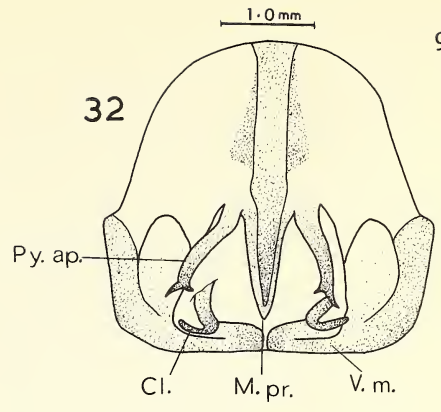
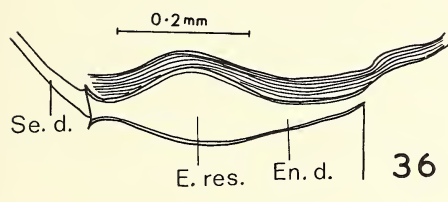
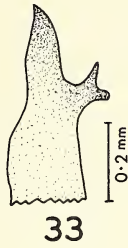
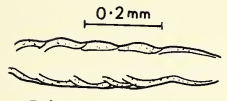
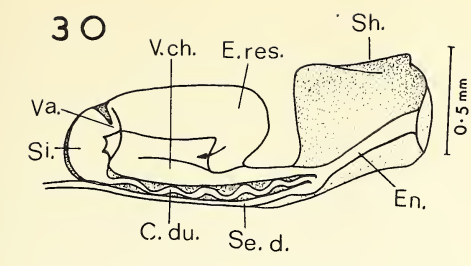




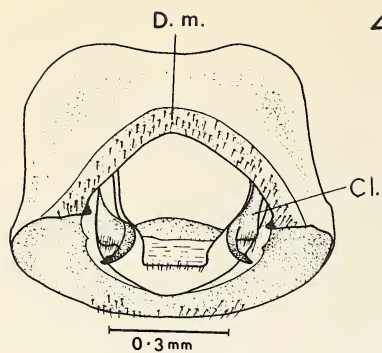


Anterior

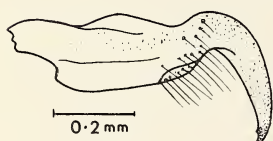




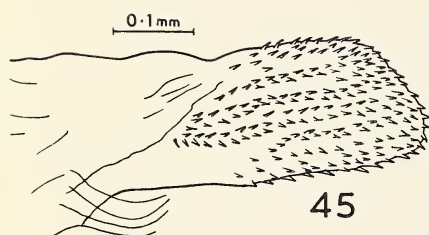
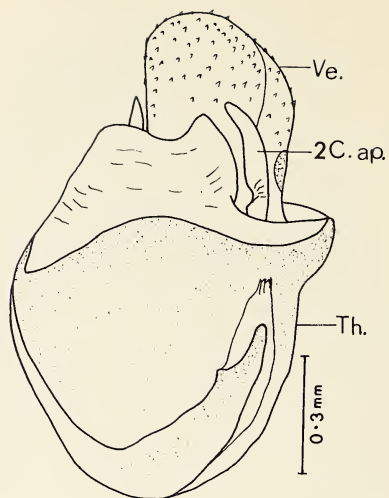




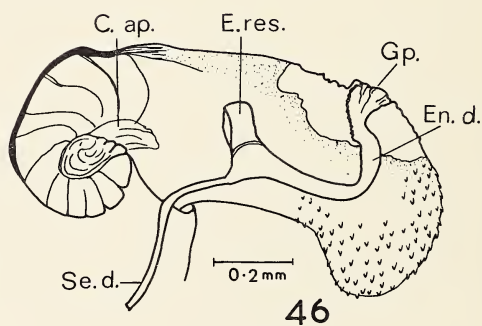
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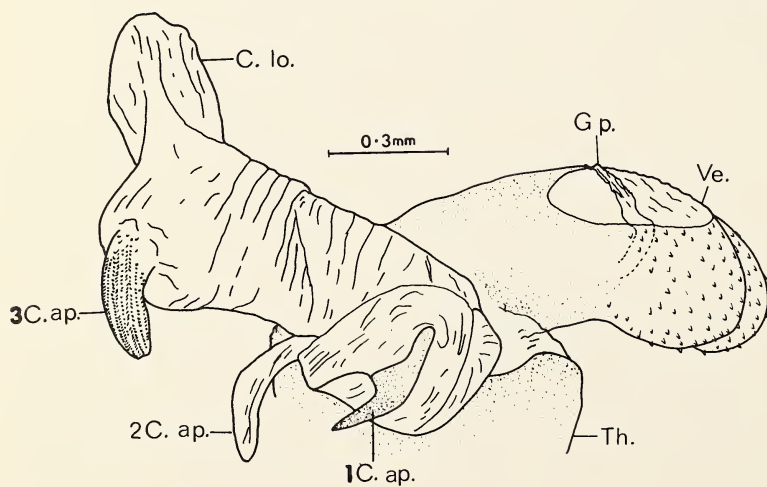
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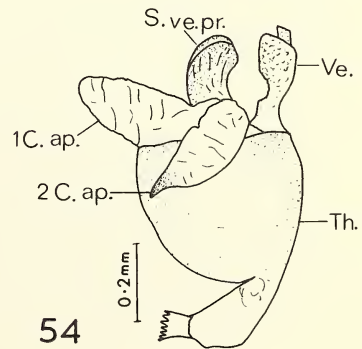
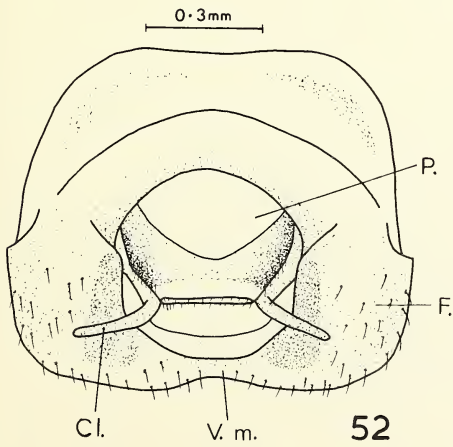
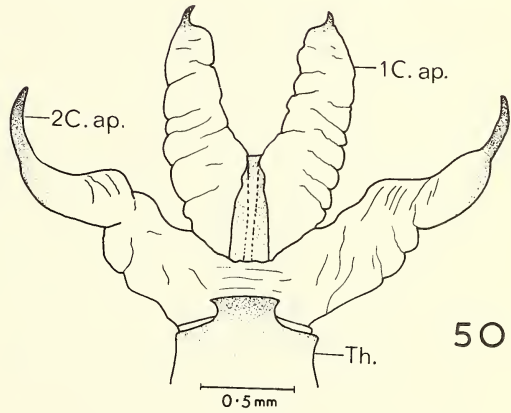
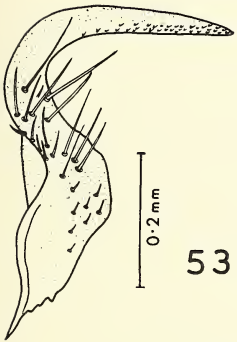
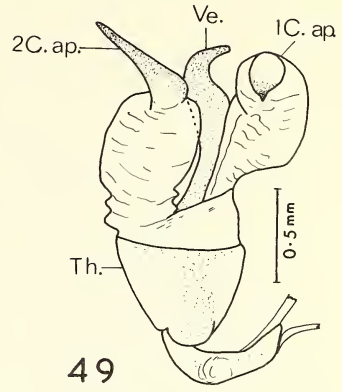
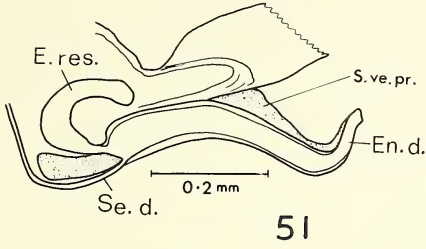
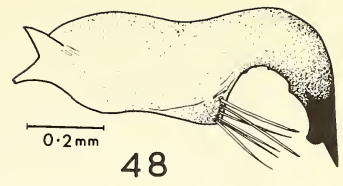
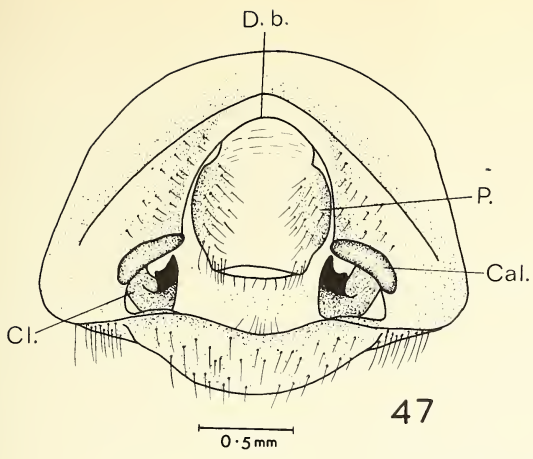
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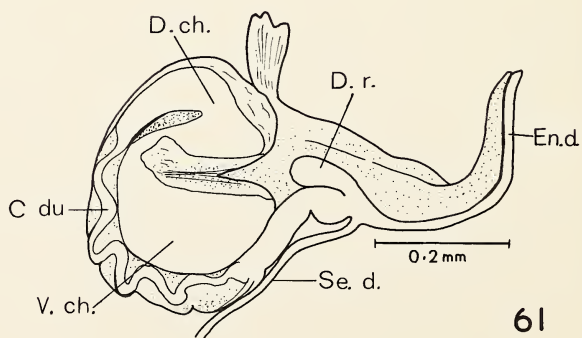
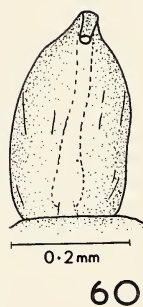
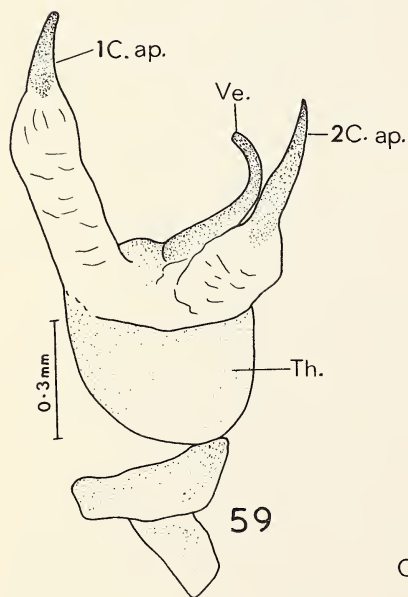
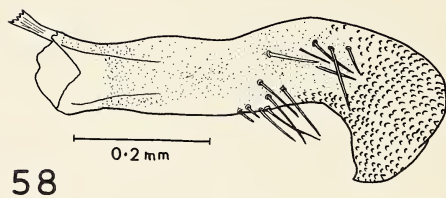
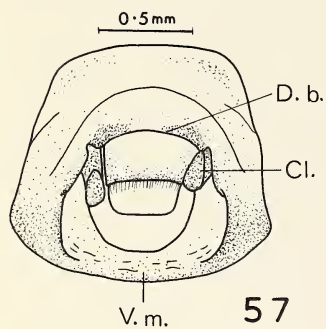
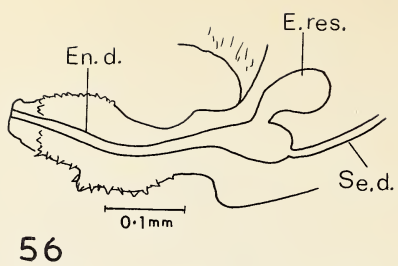
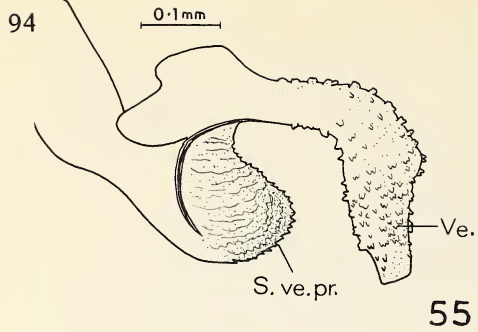


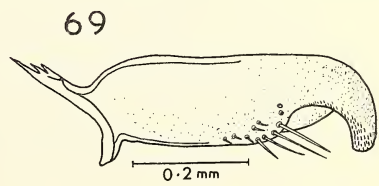
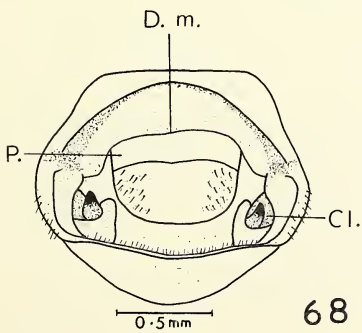
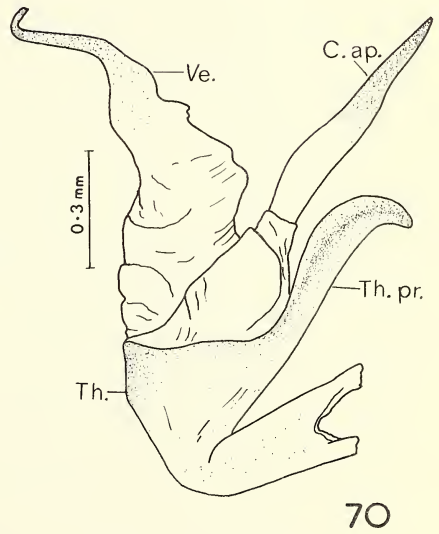
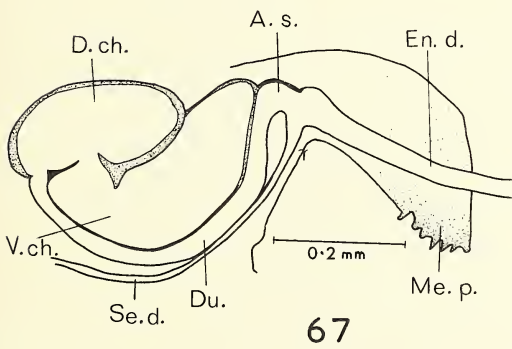
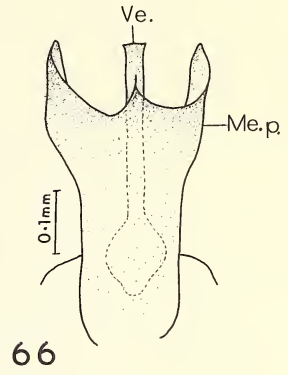
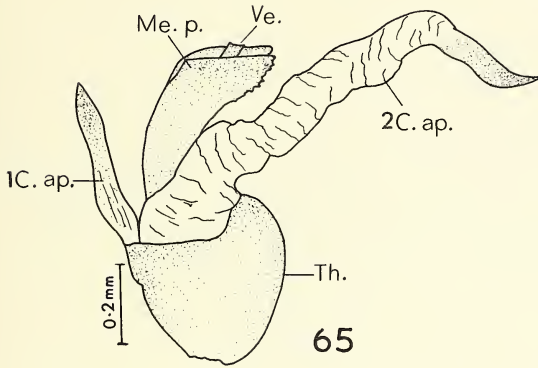
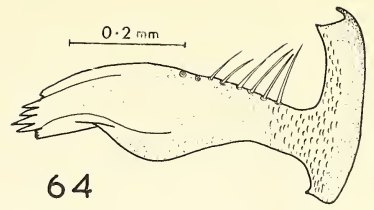
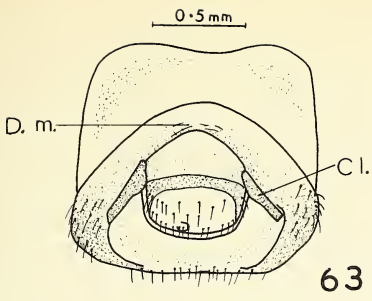
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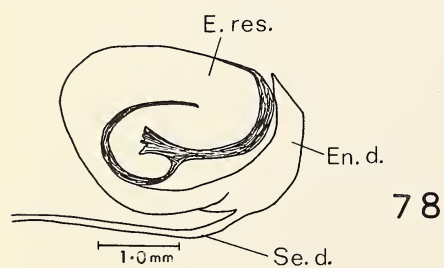
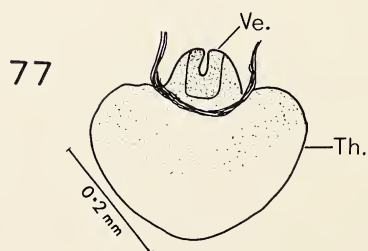
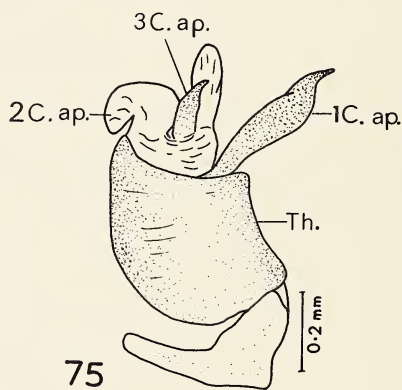
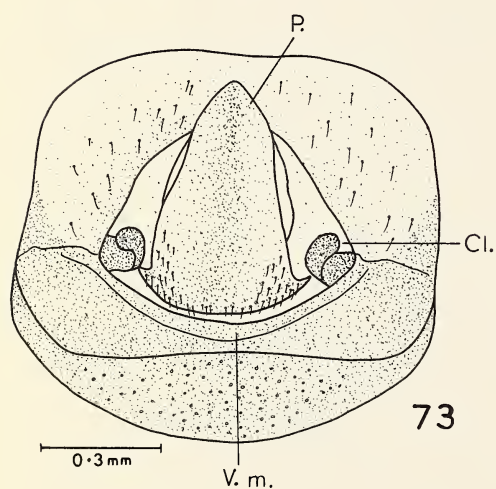
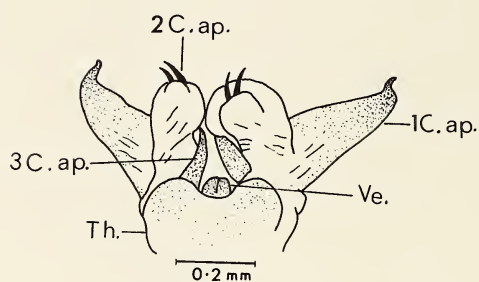
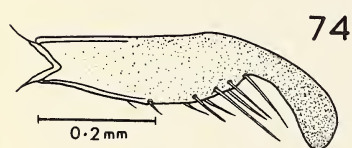
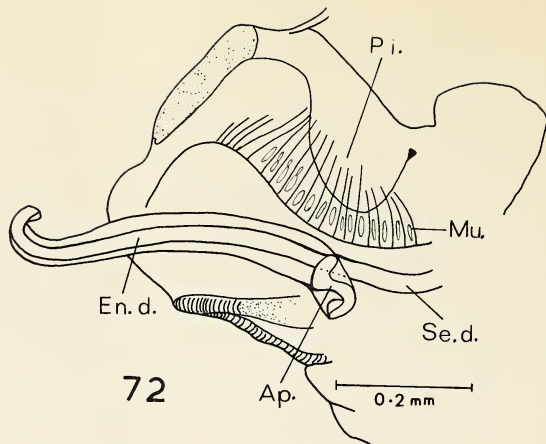
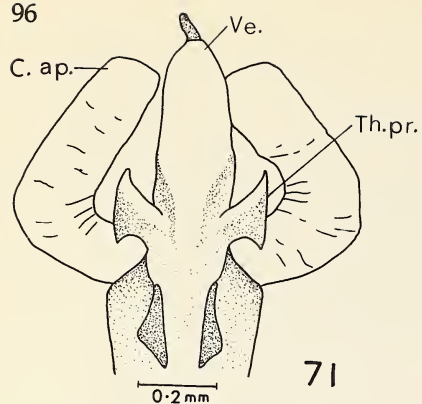
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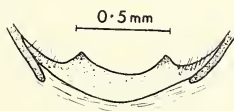
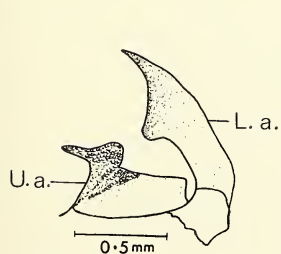
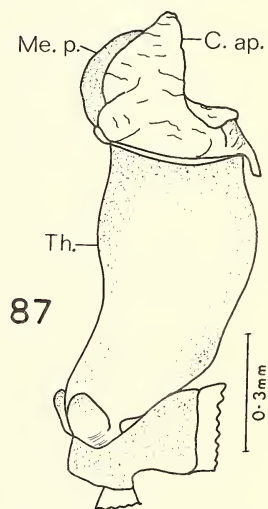
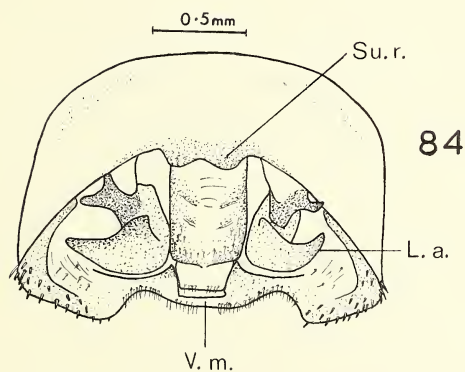
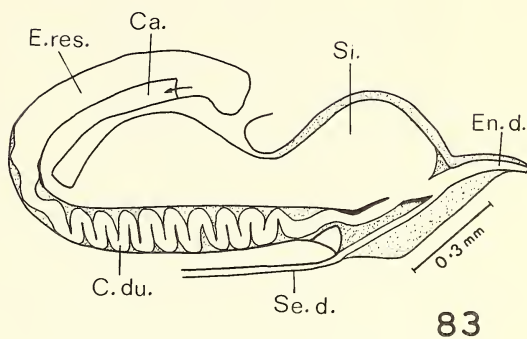
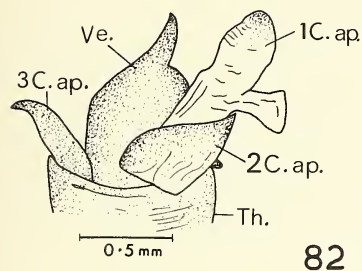
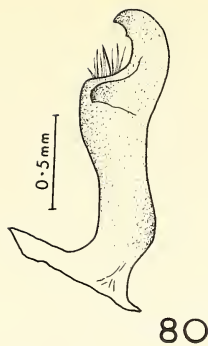
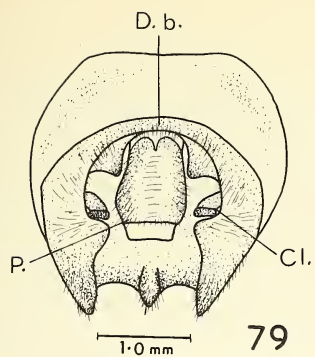






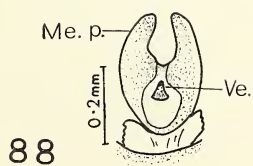




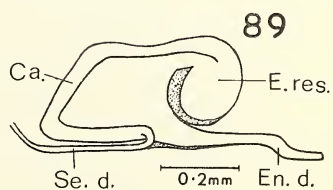


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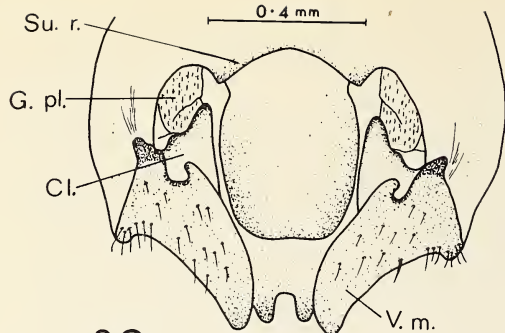


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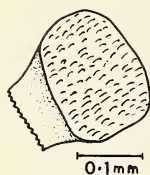
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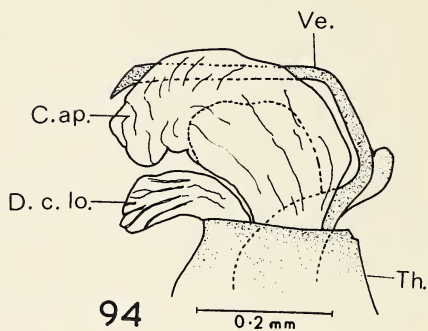


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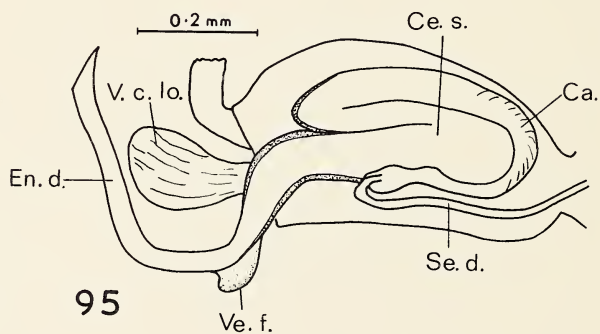
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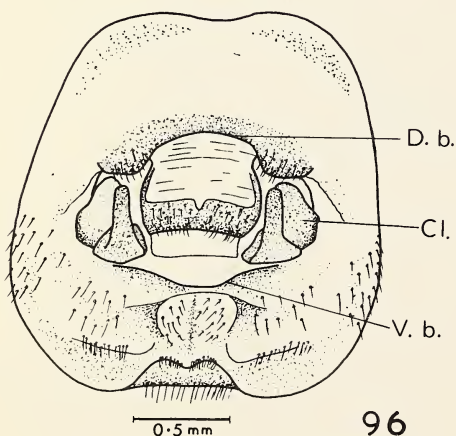
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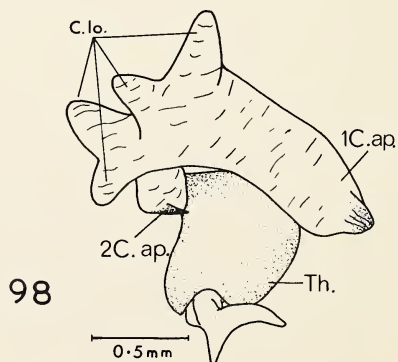
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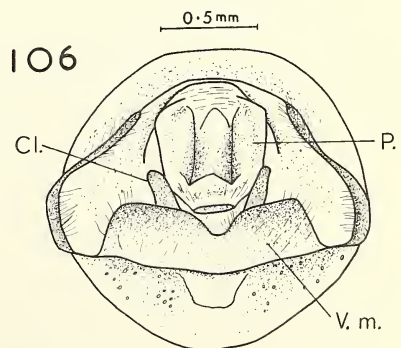
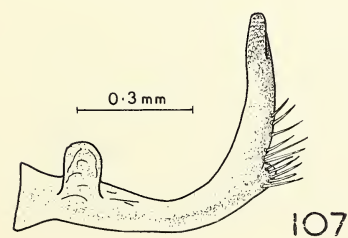
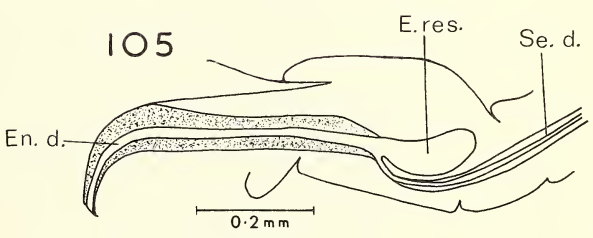
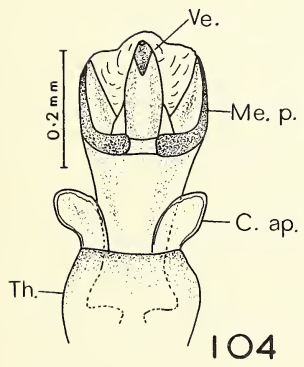
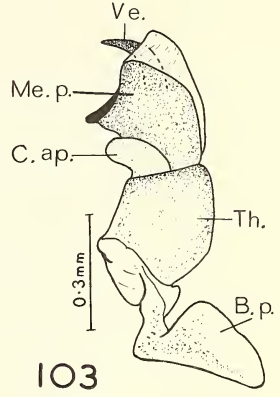
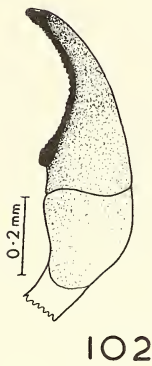
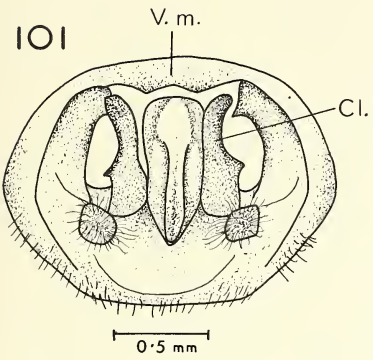
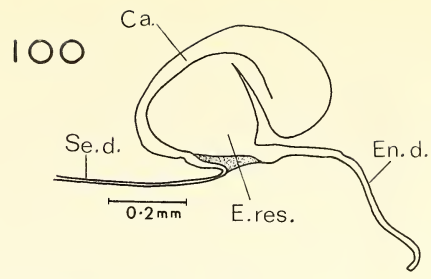
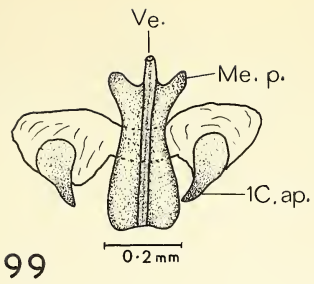
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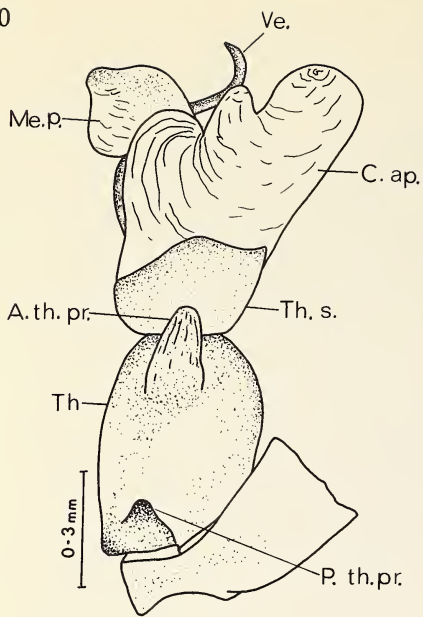
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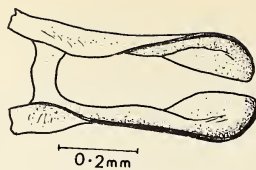
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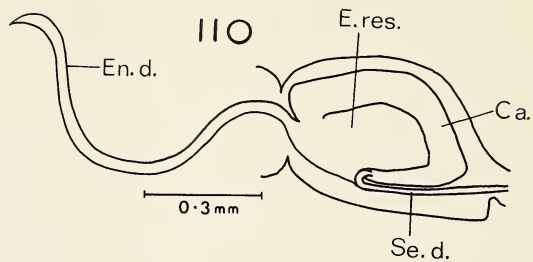




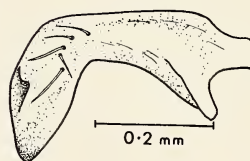
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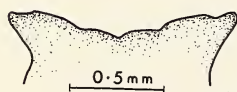
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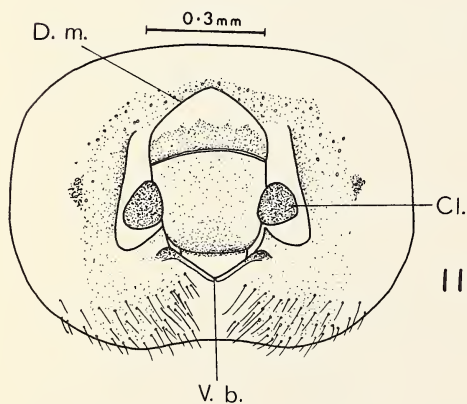
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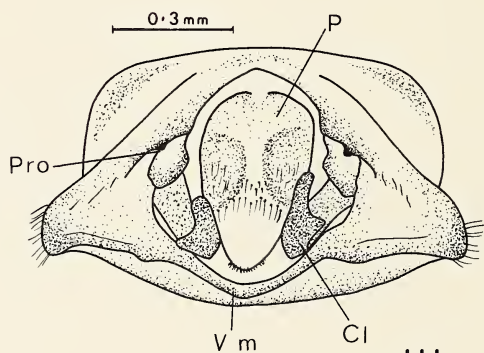
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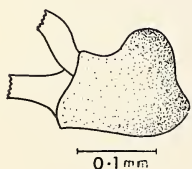
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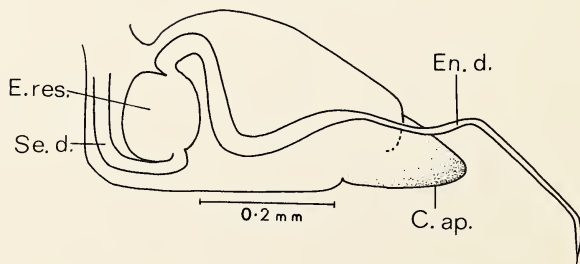
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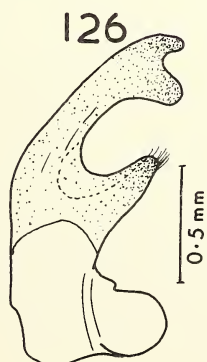
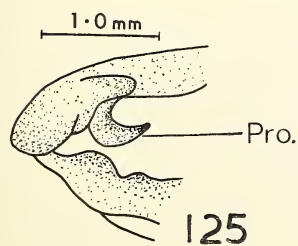
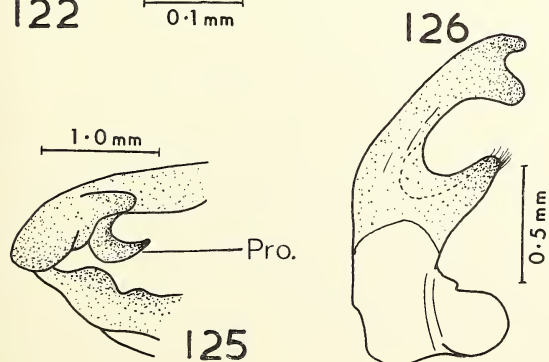
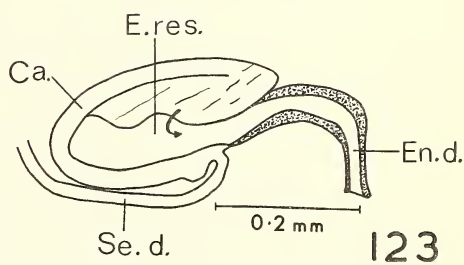
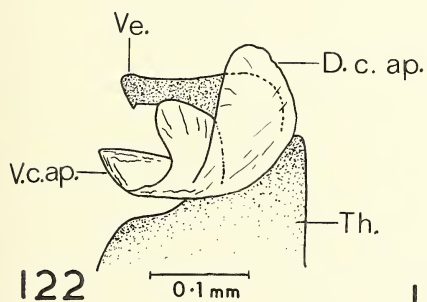
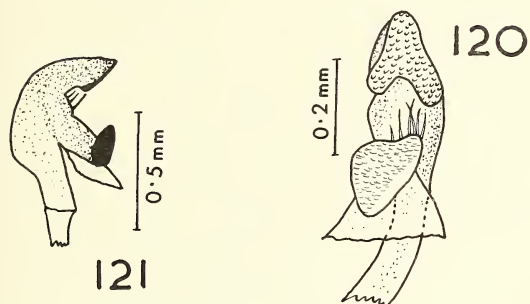
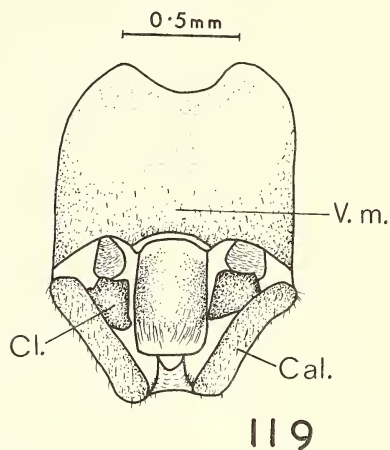
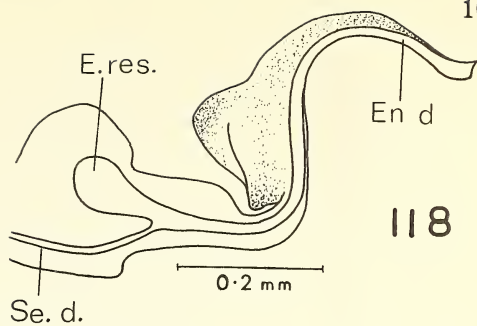
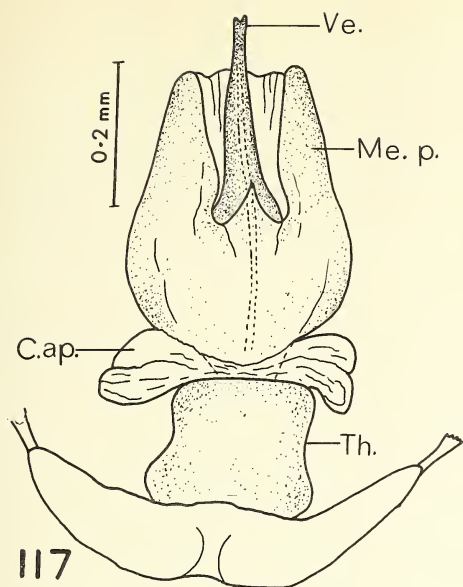
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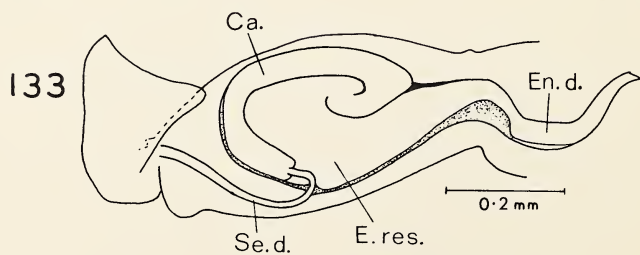
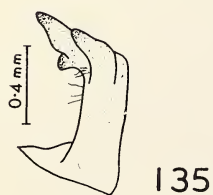
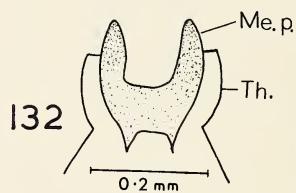
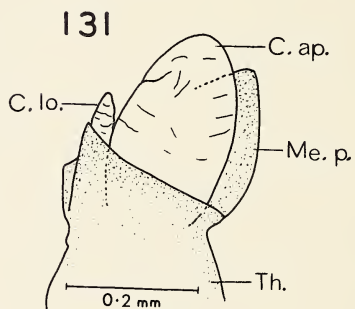
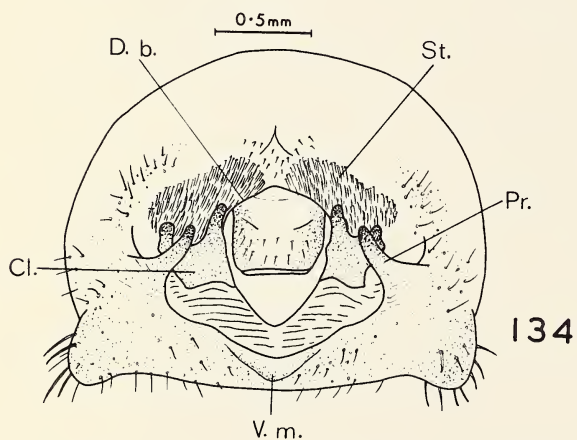
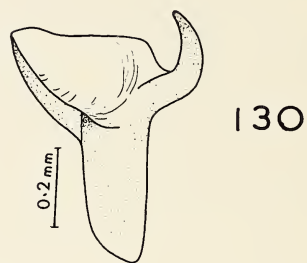
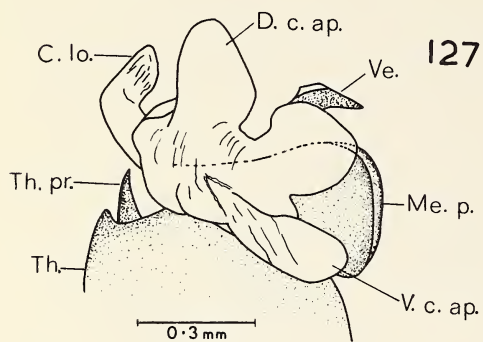
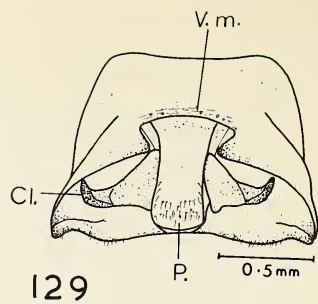
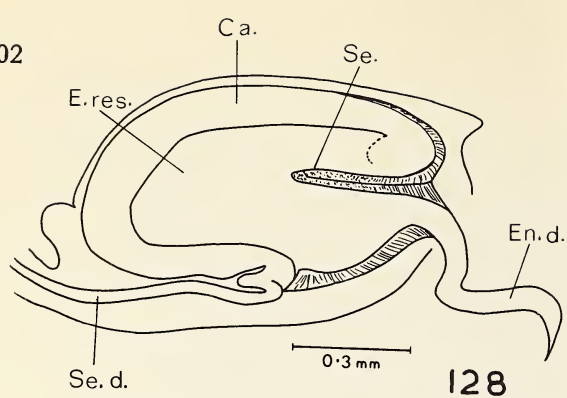


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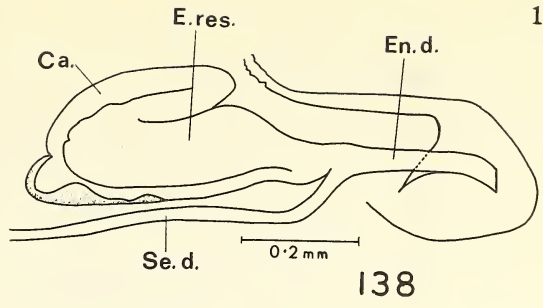
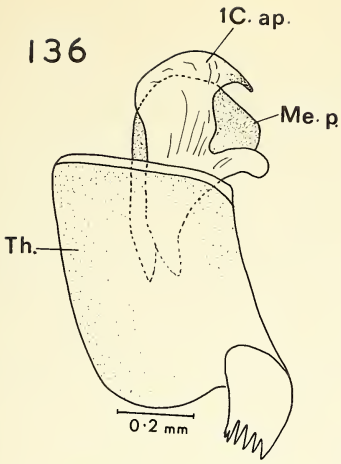


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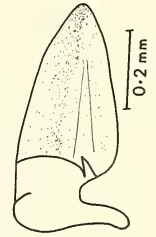
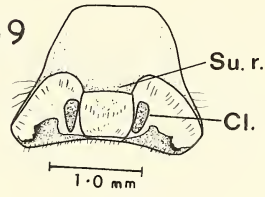


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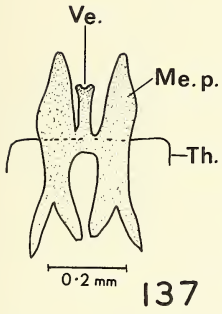


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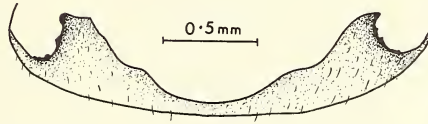
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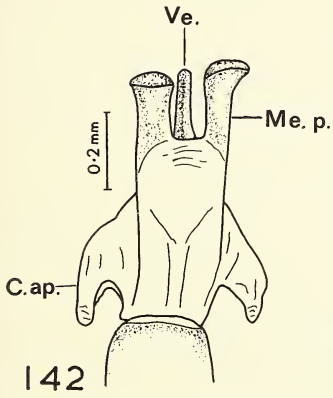
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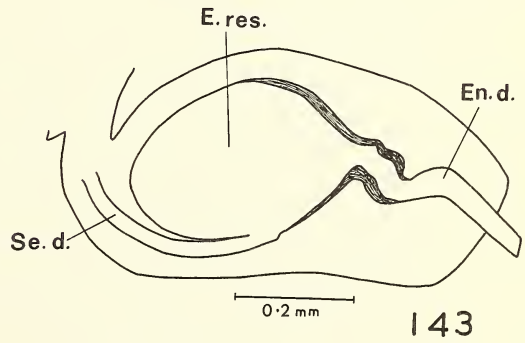
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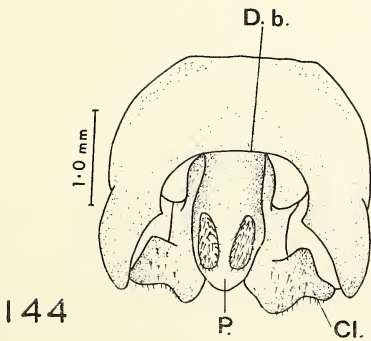
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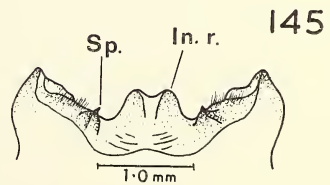
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143

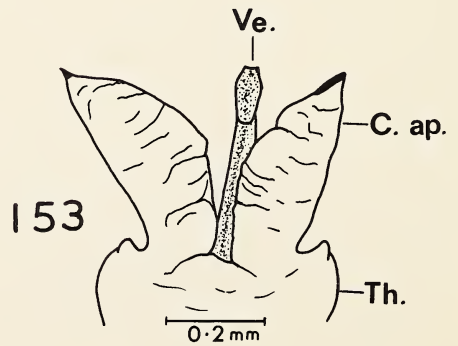
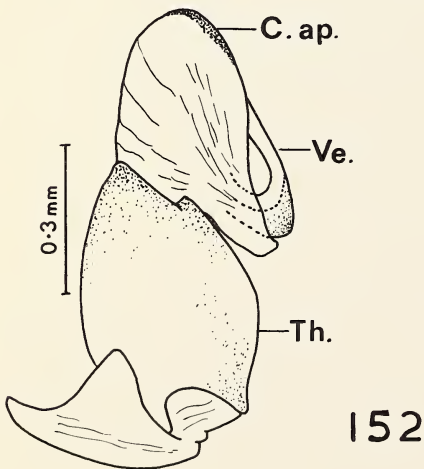
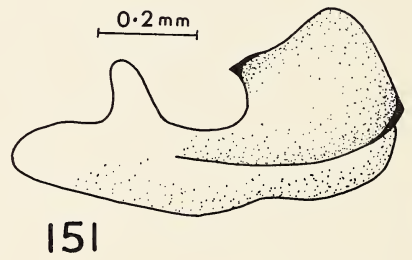
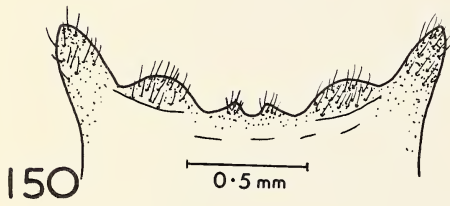
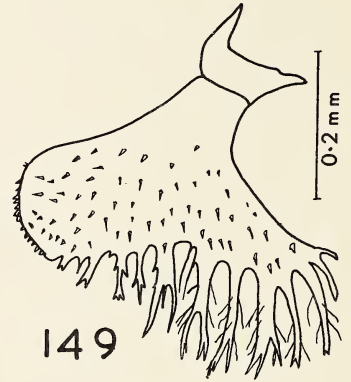
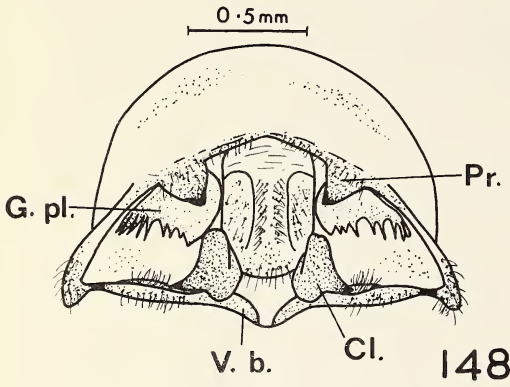
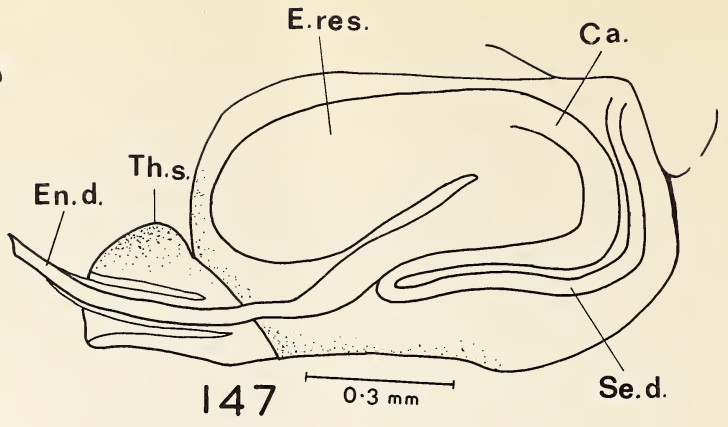
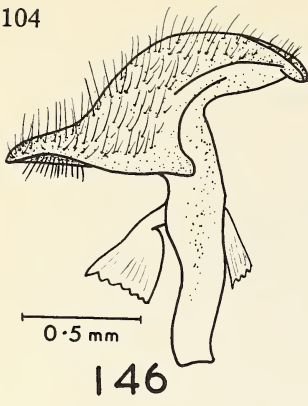


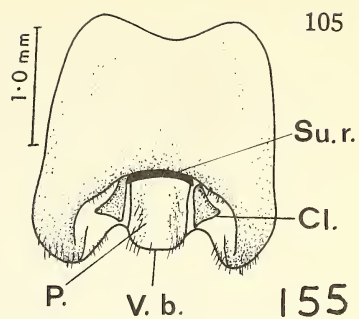
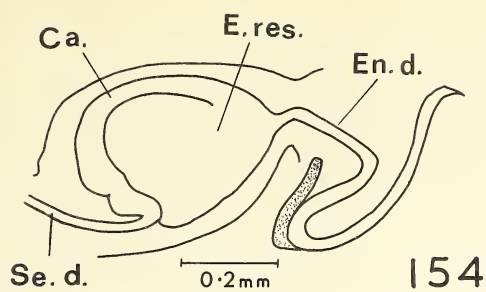
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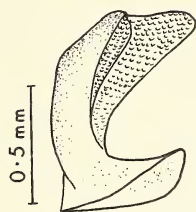
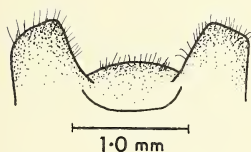
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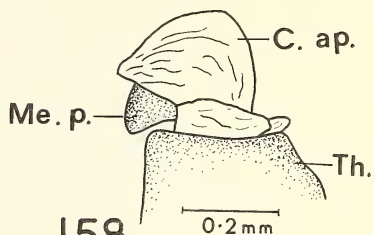




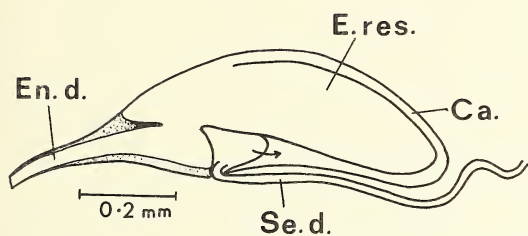
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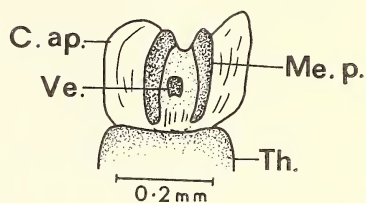
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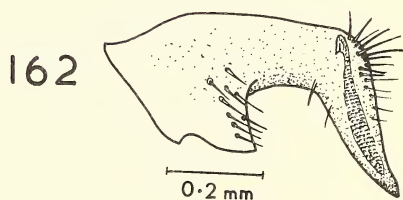
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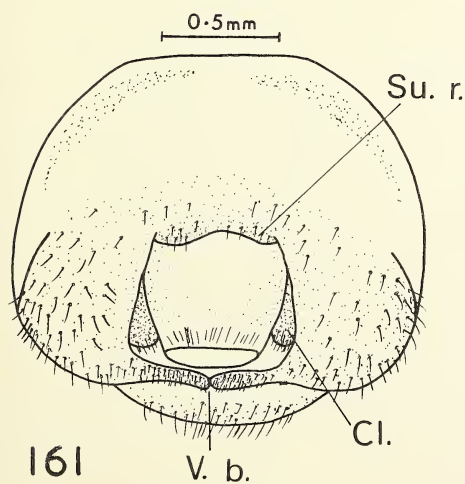
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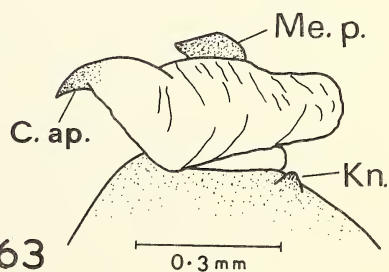
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162

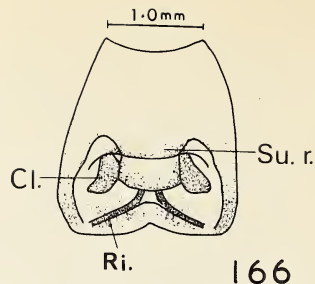
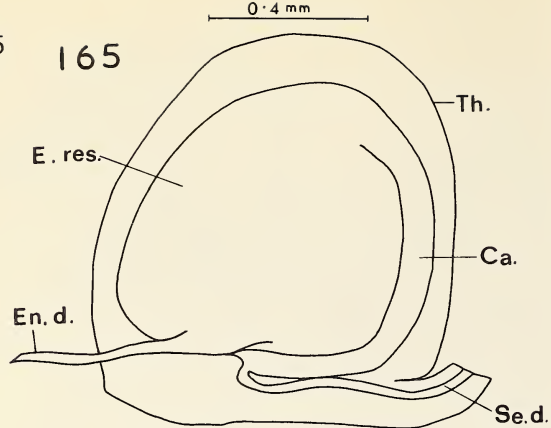


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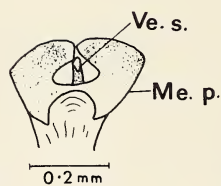


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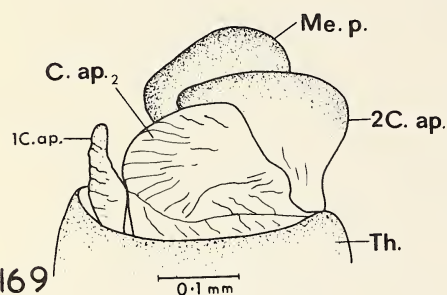
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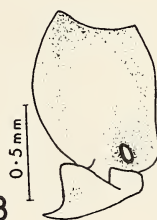
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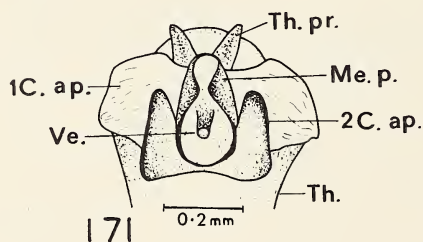
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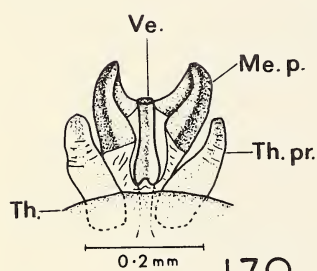
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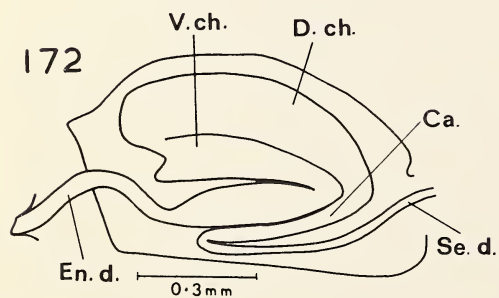
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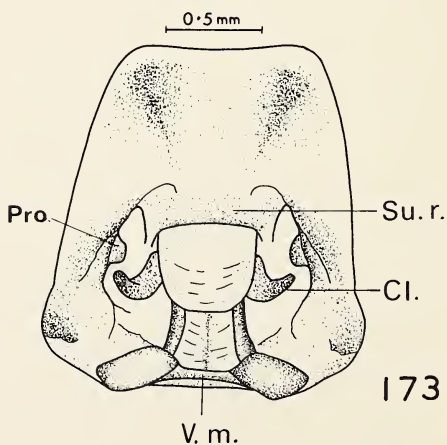
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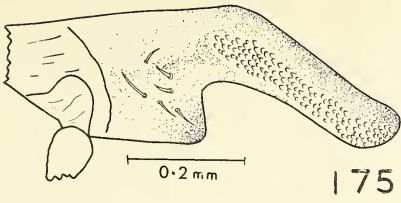


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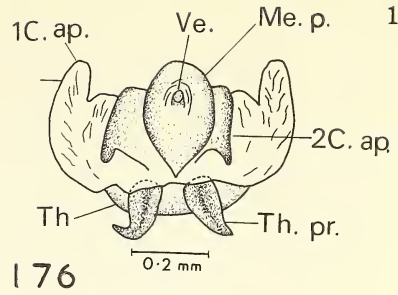


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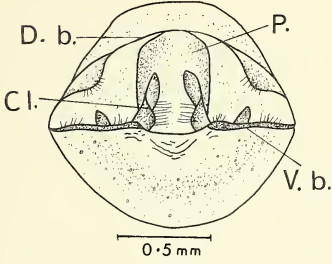




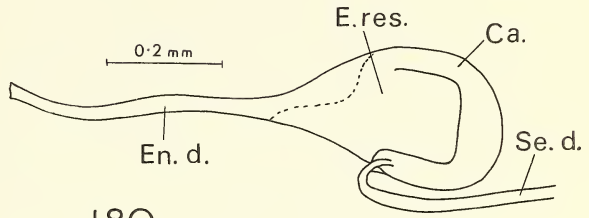
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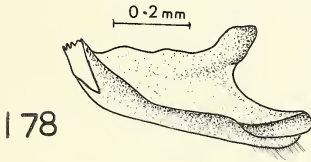
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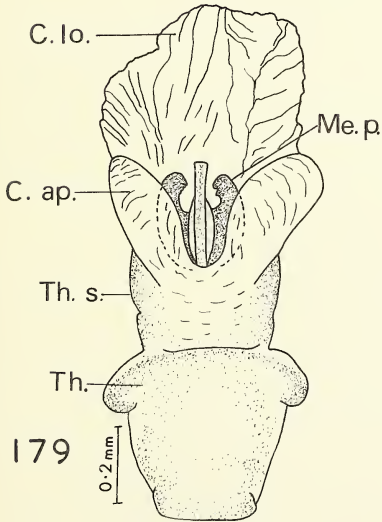
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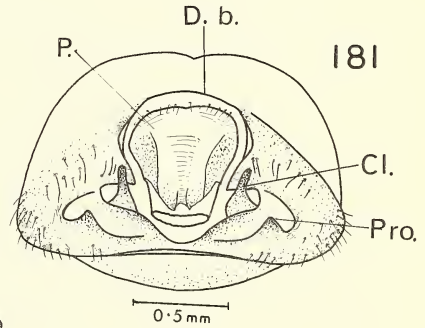
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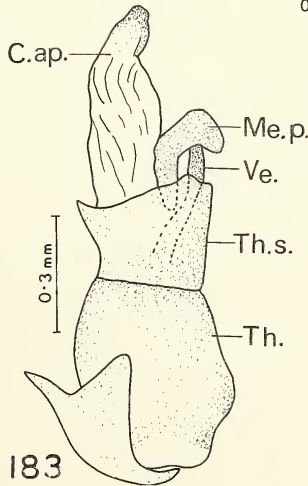
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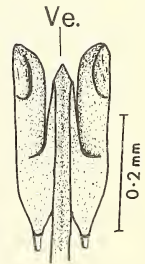
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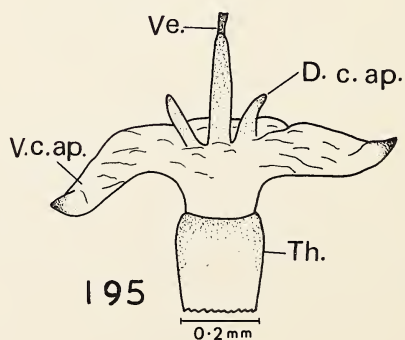
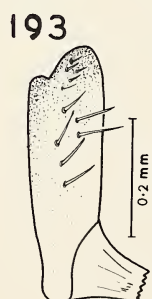
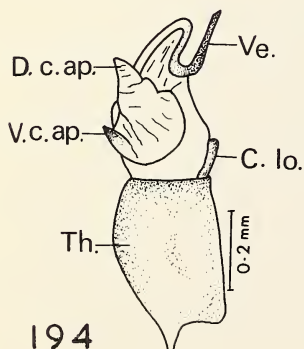
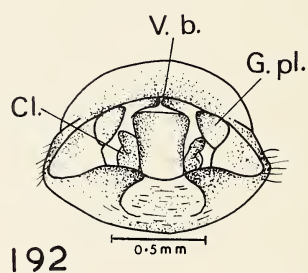
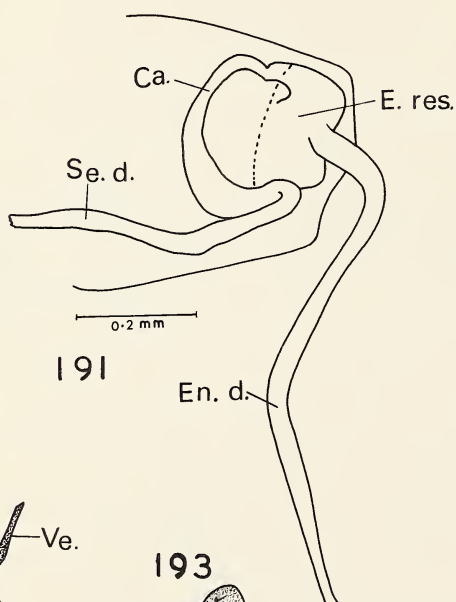
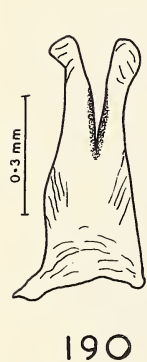
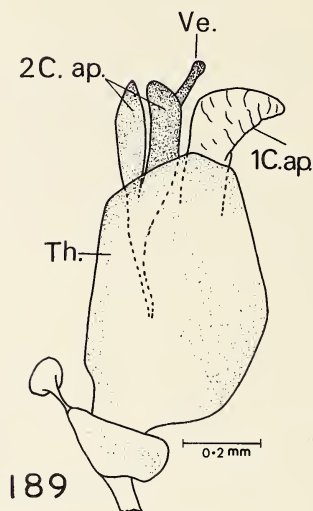
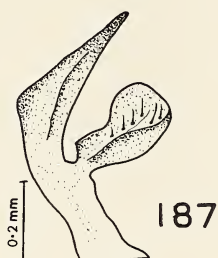
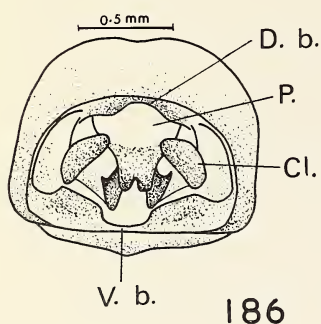
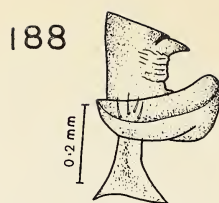
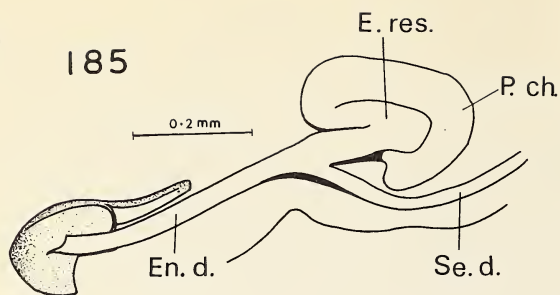


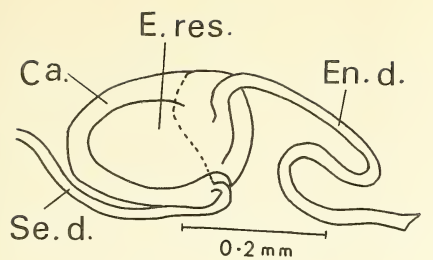
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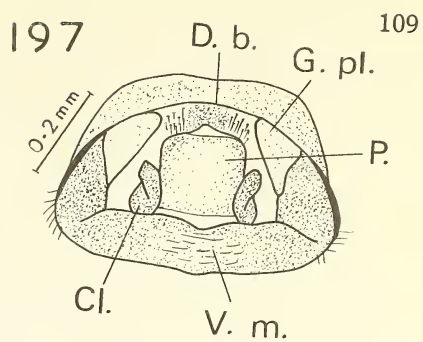
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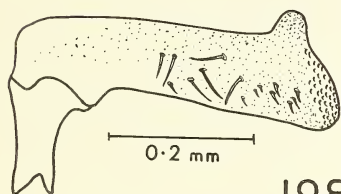


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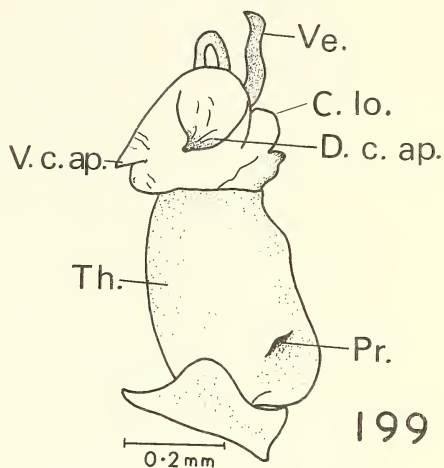


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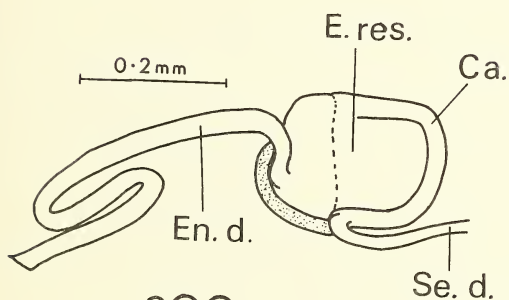
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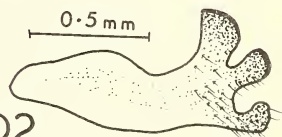
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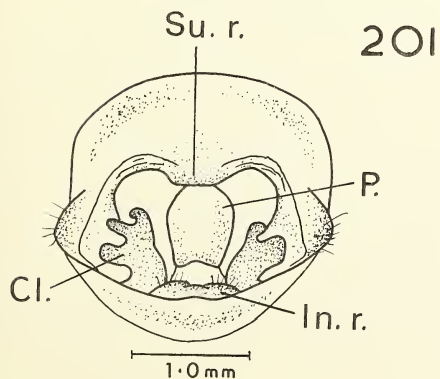
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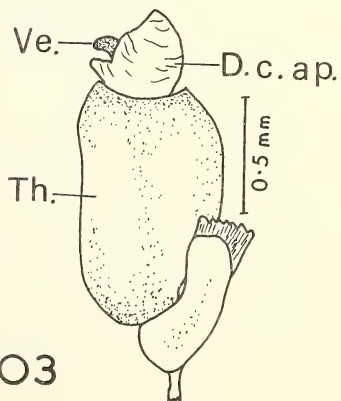
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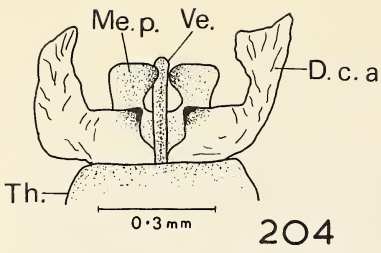
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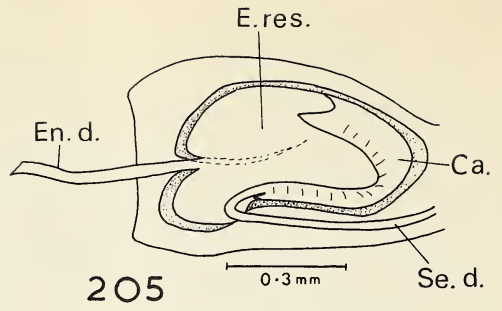
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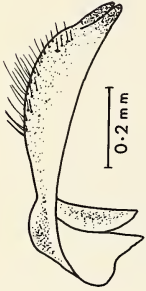
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204



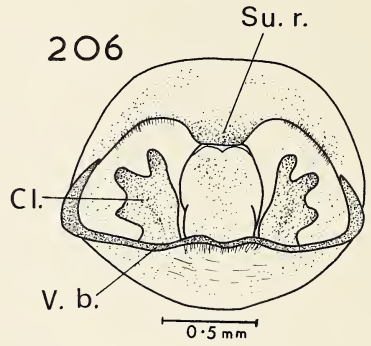
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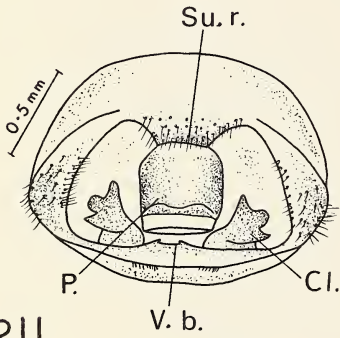
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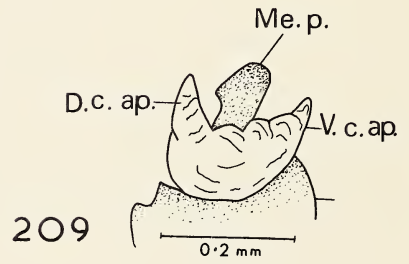
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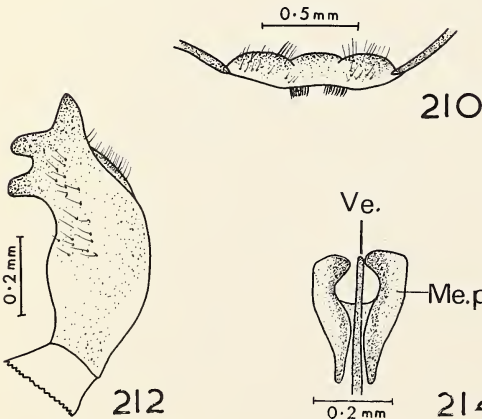
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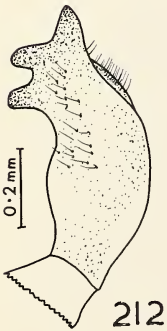
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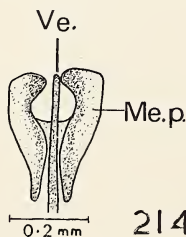
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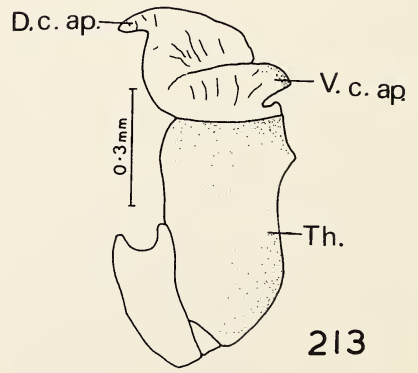
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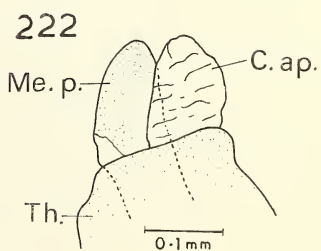
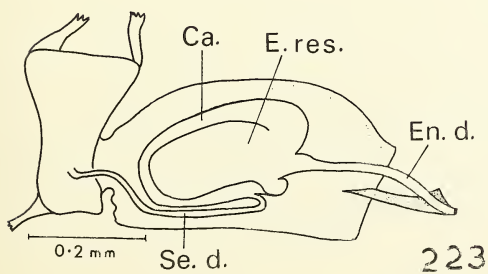
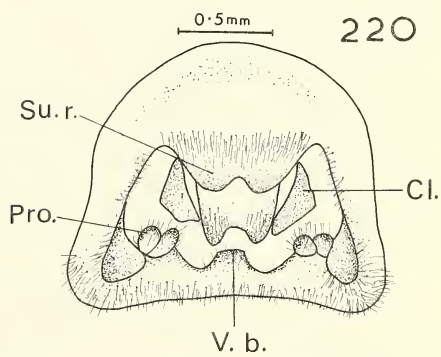
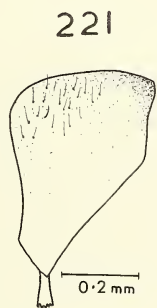
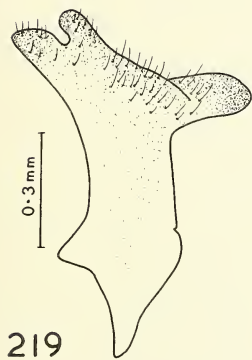
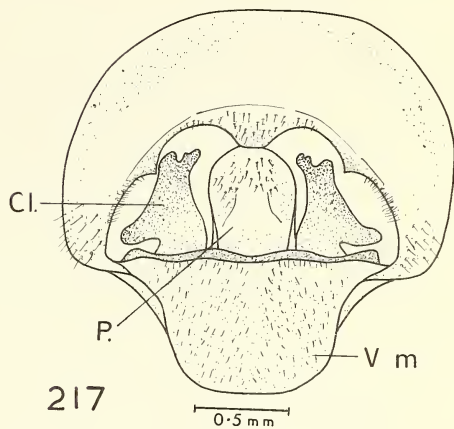
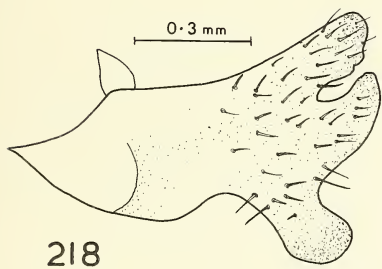
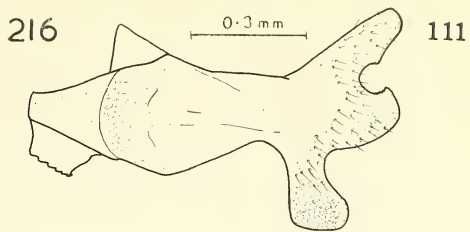
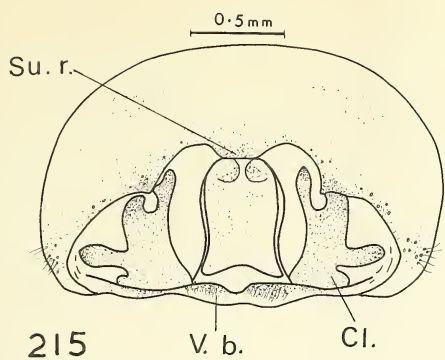
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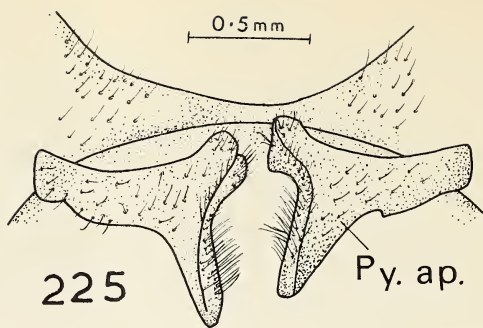
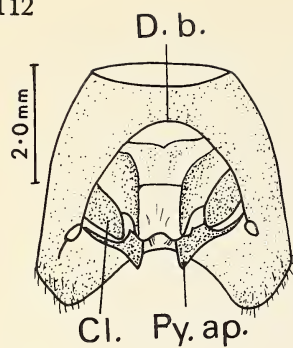
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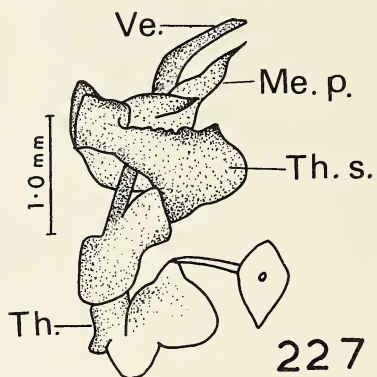
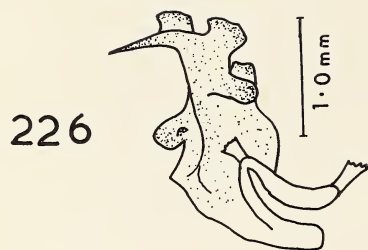
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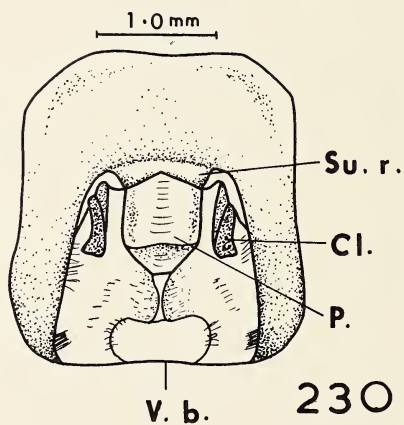
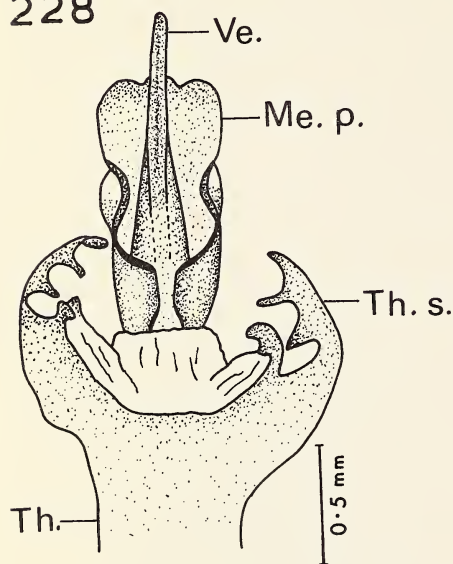




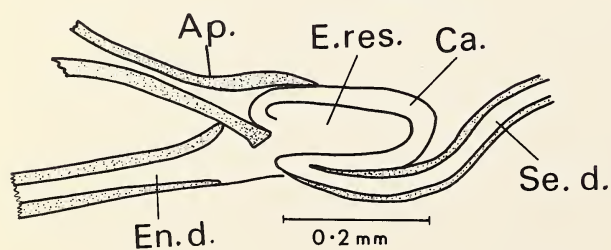
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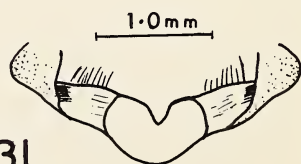
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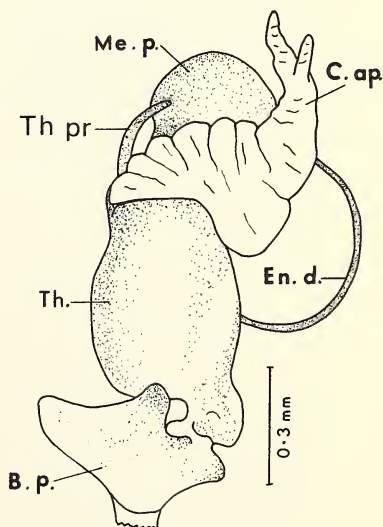
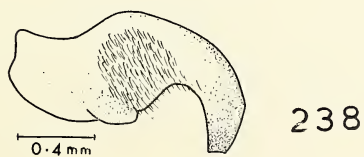
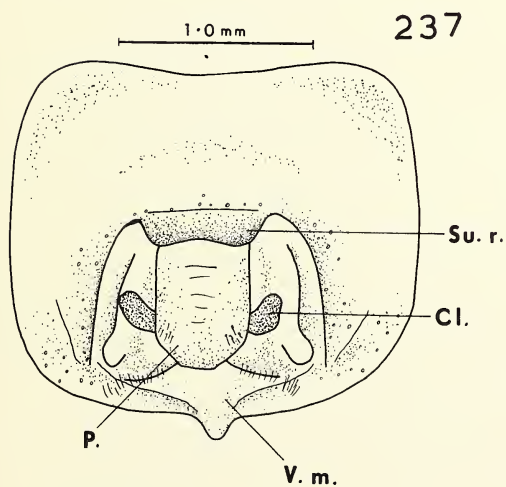
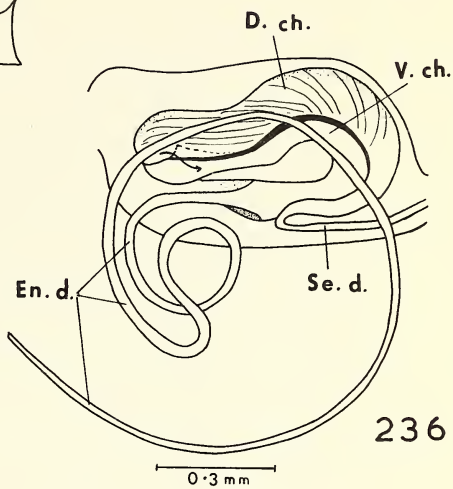
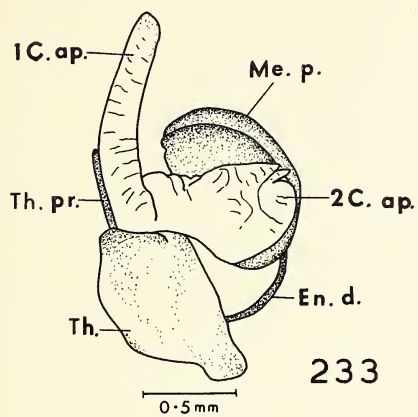
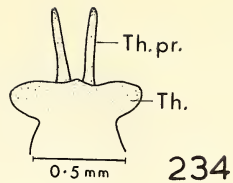
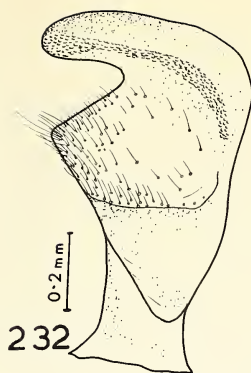
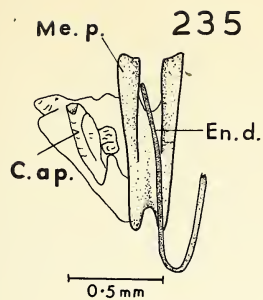


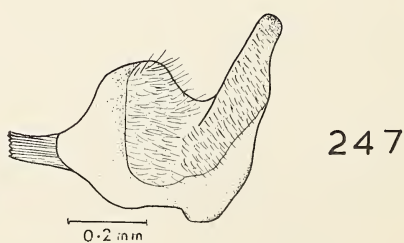
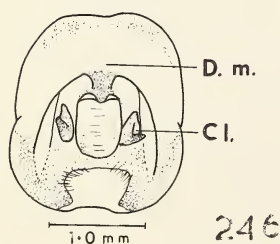
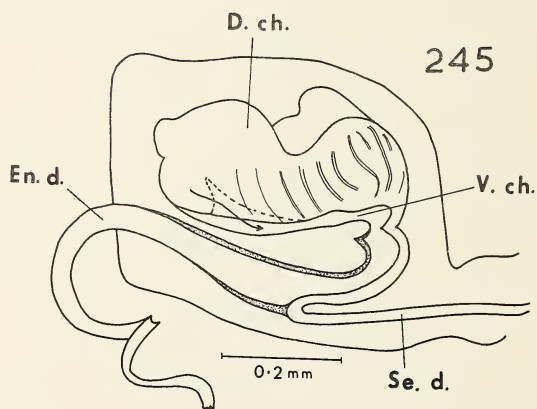
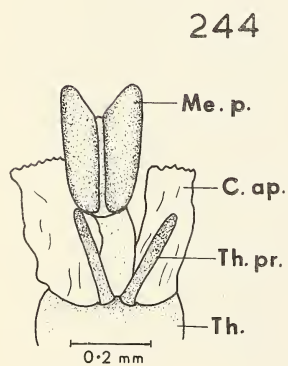
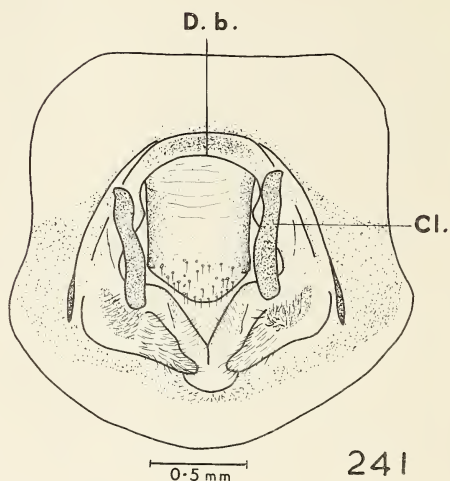
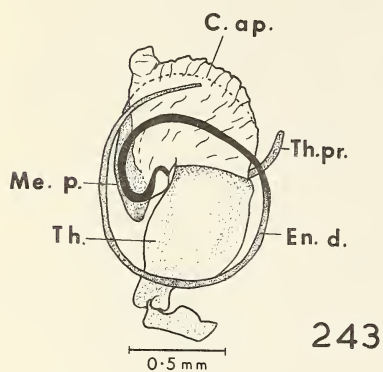
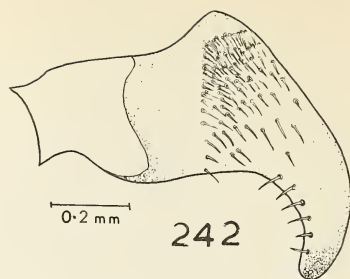
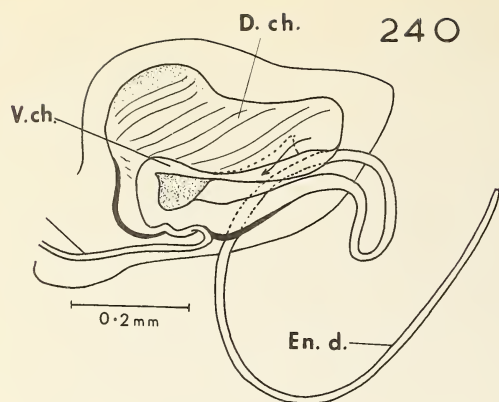
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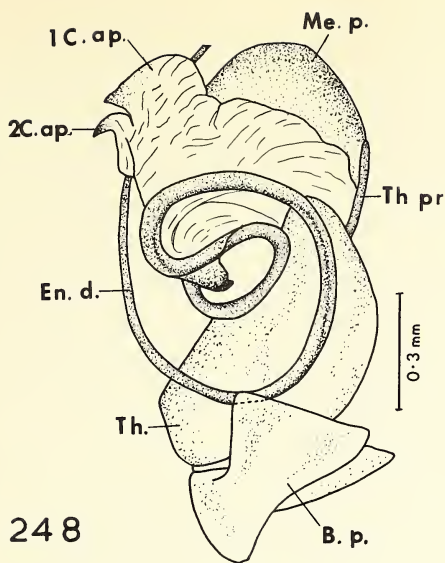


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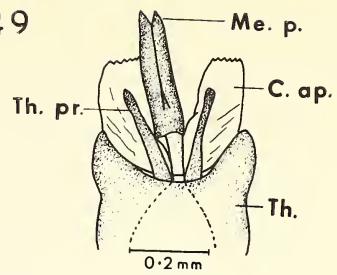






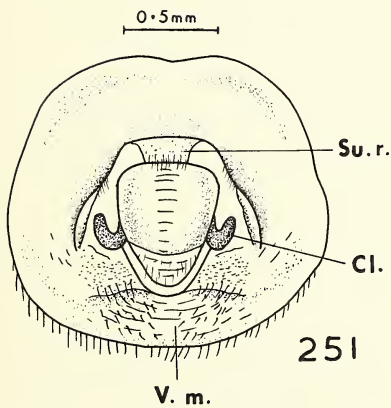
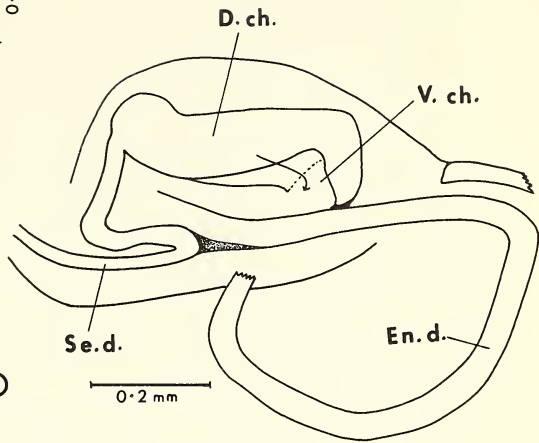


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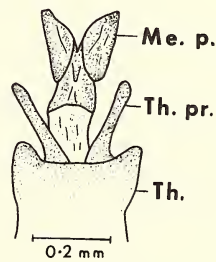


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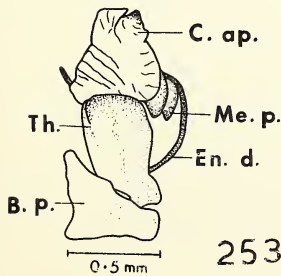
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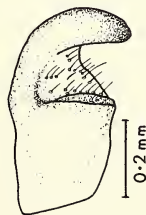
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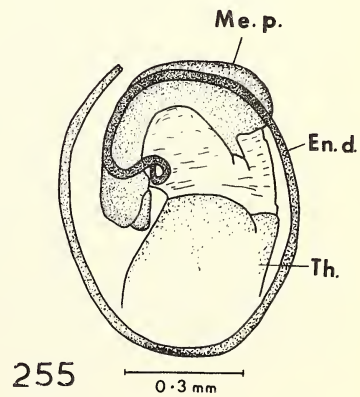
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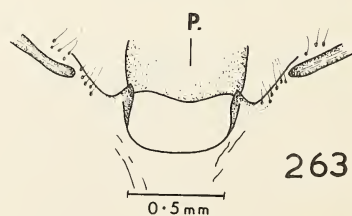
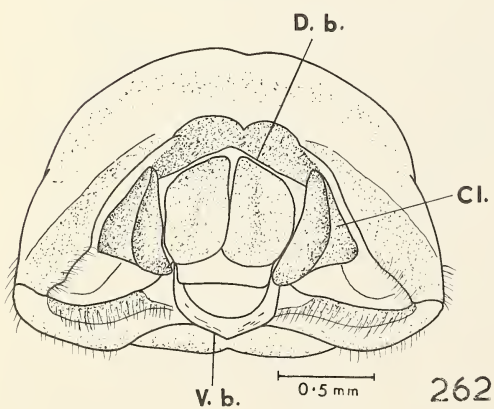
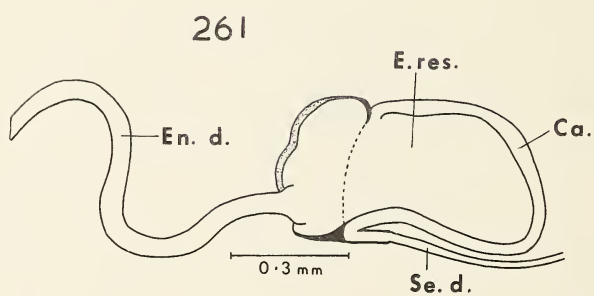
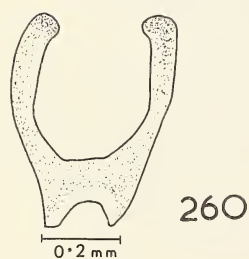
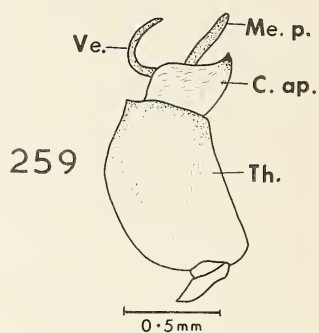
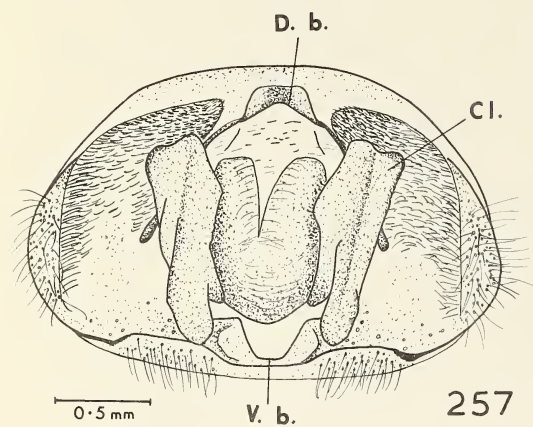
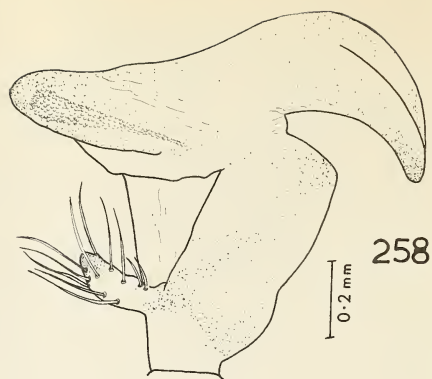
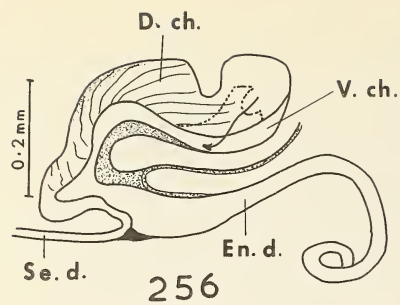


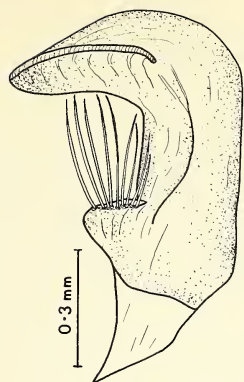
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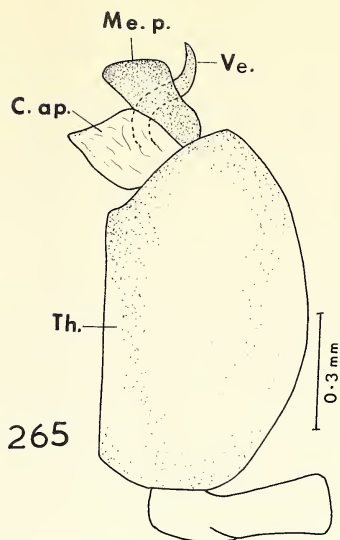
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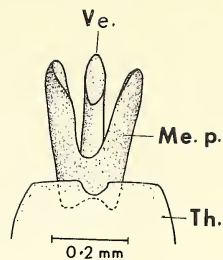




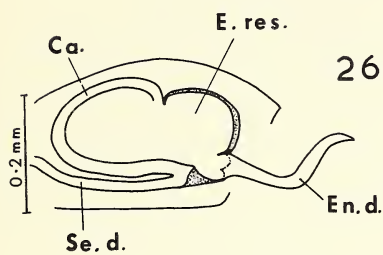
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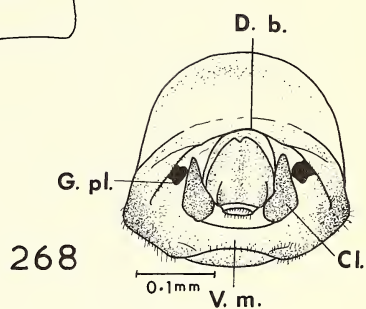
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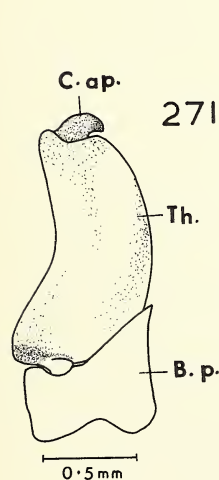
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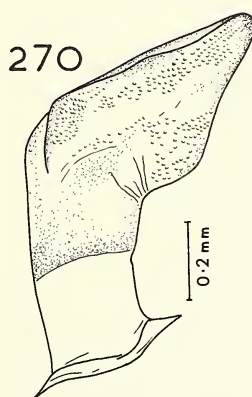
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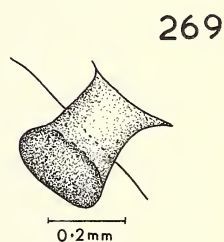
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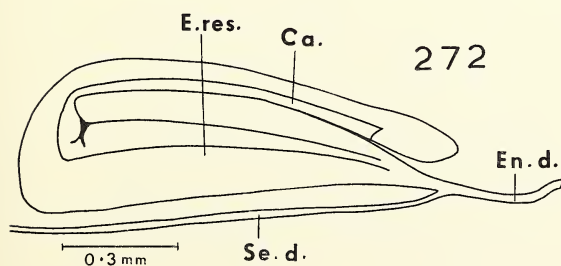
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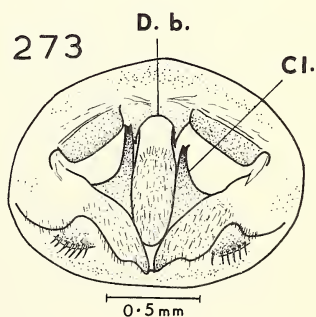
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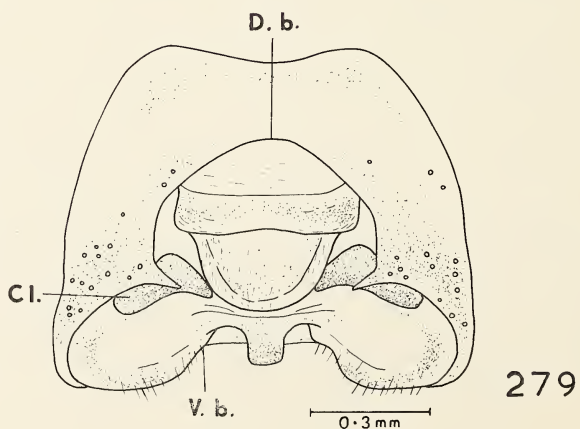
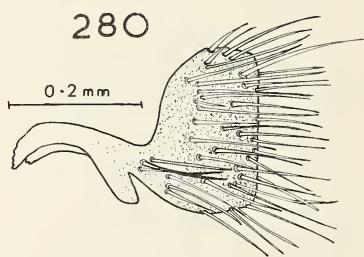
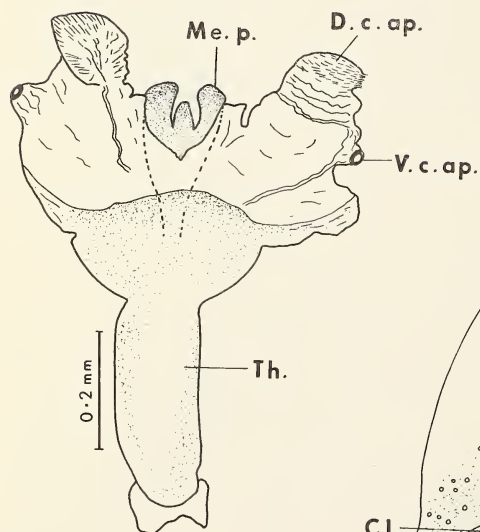
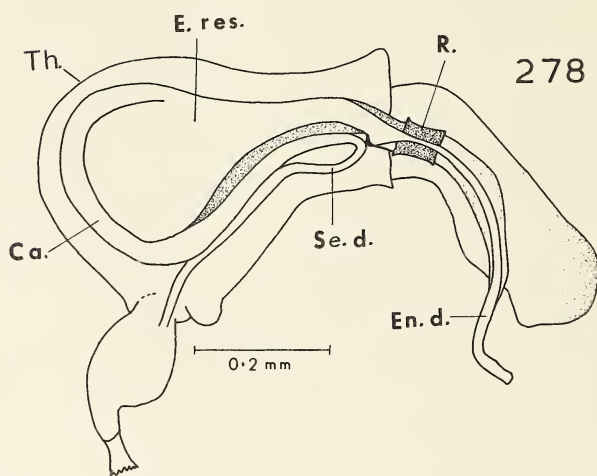
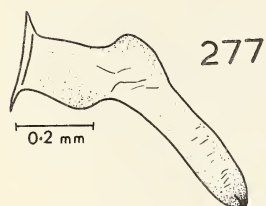
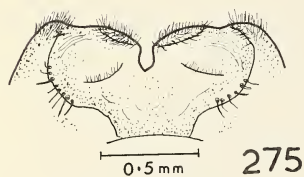
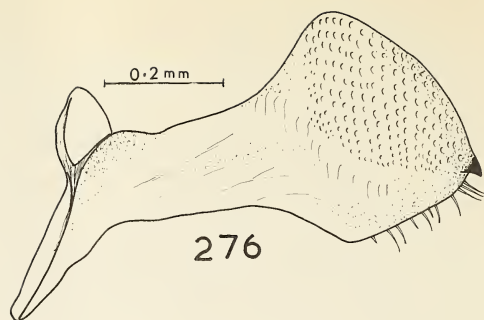
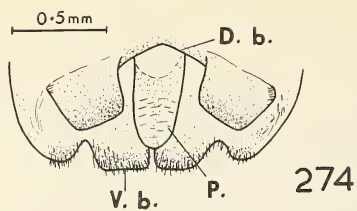
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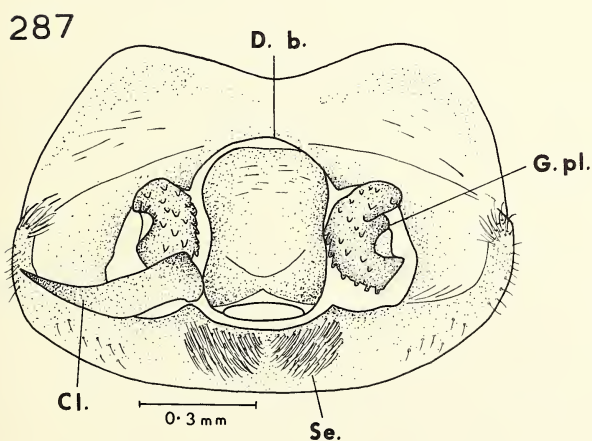
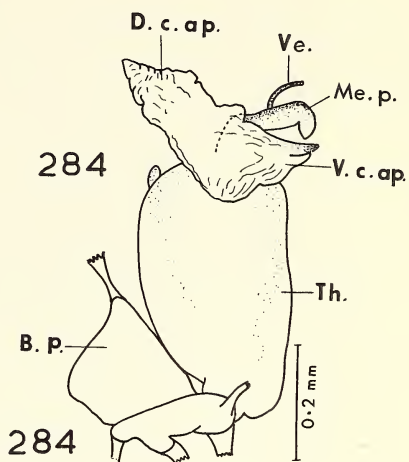
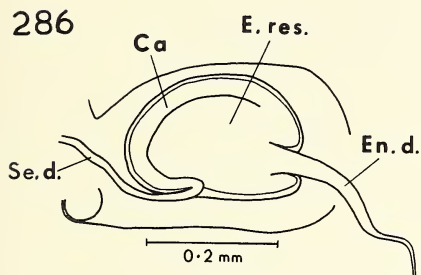
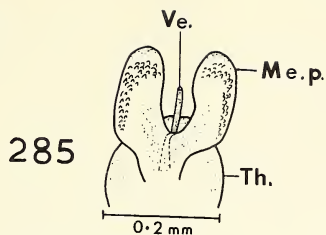
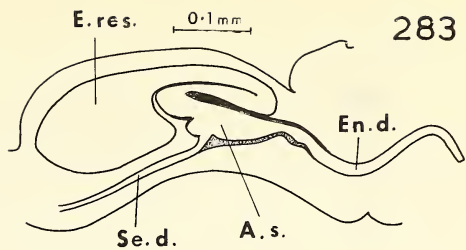
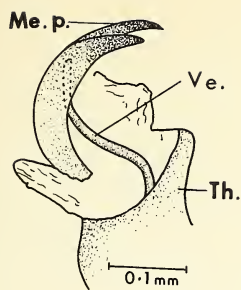


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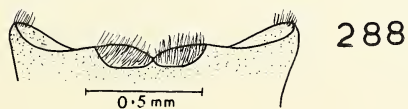
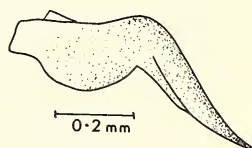


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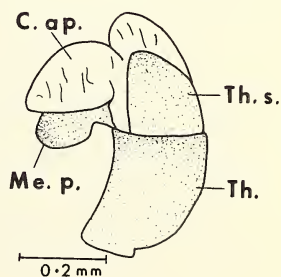




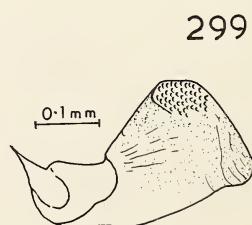
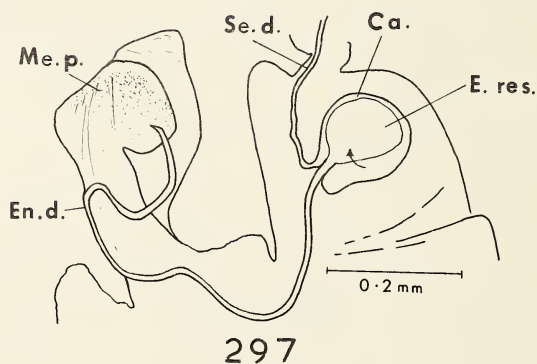
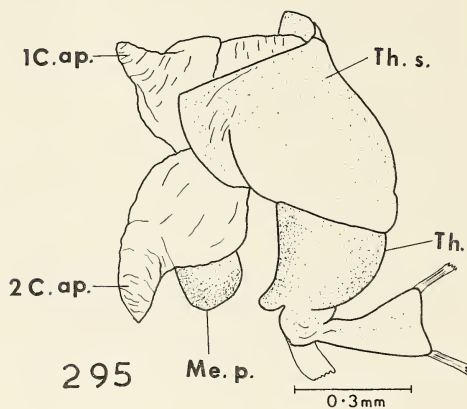
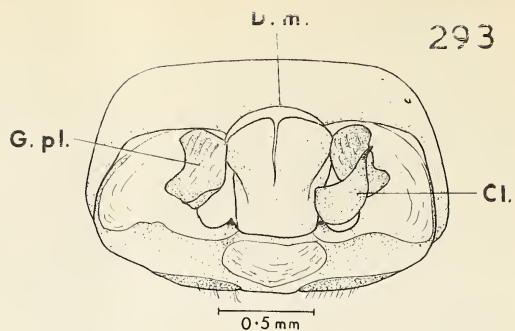
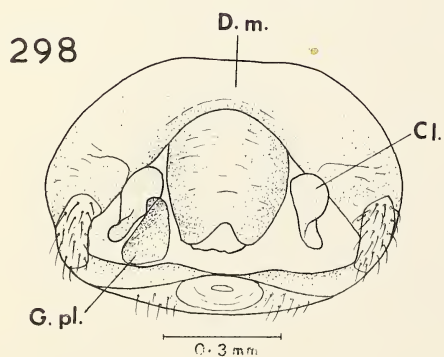
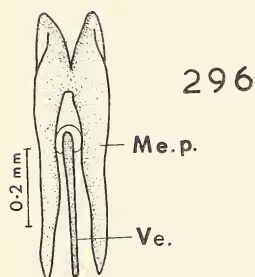
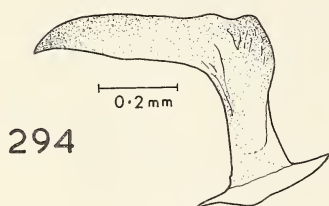
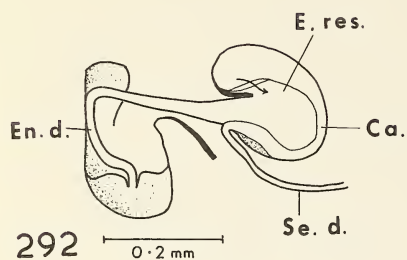
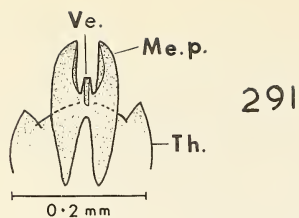
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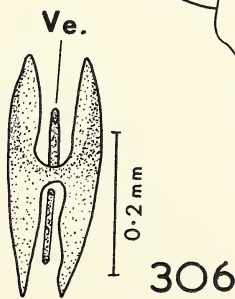
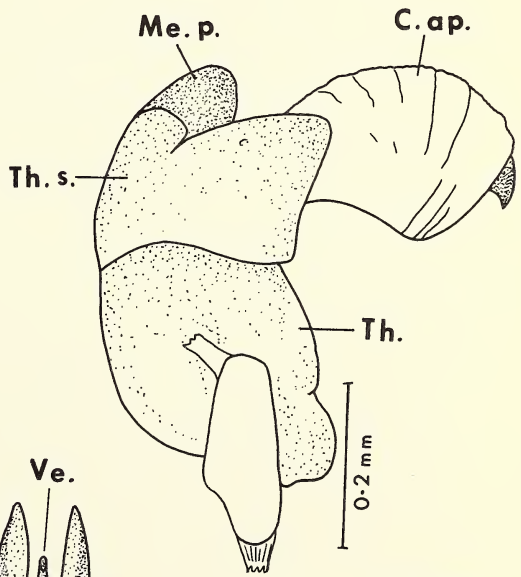
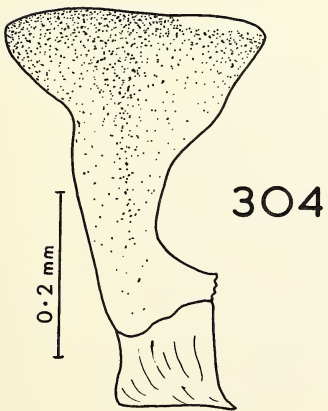
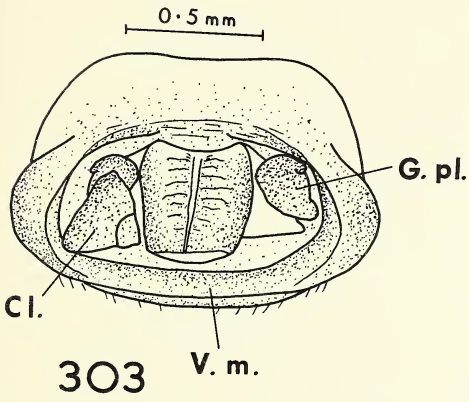
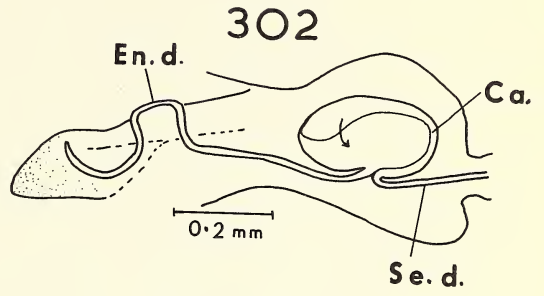
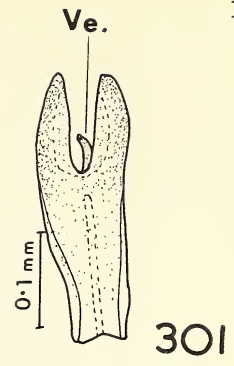
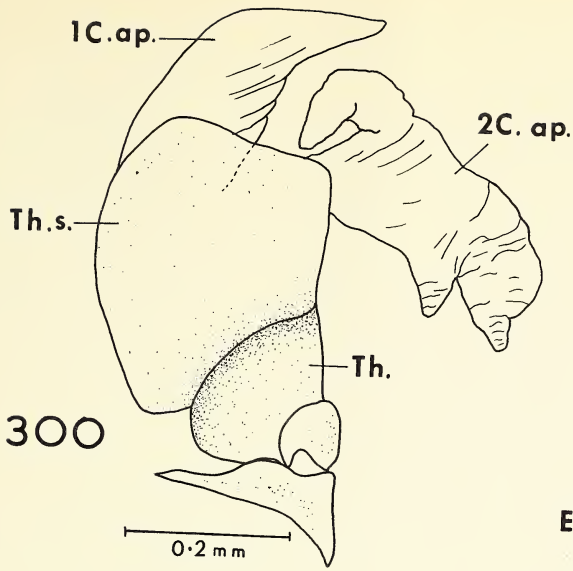


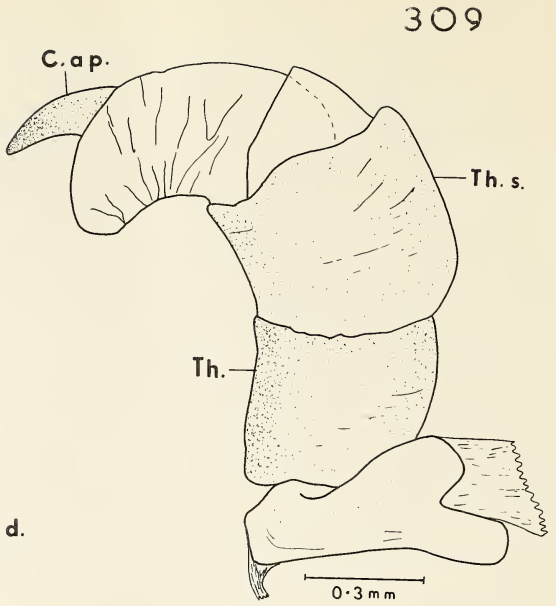
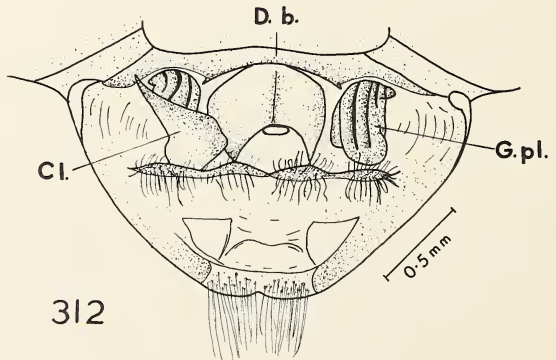
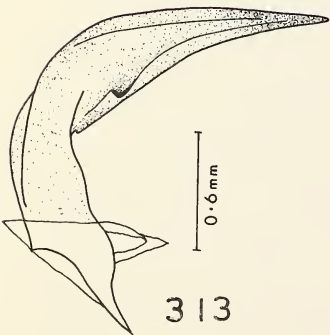
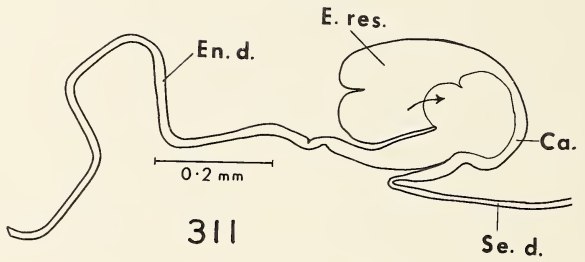
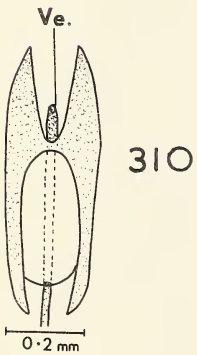
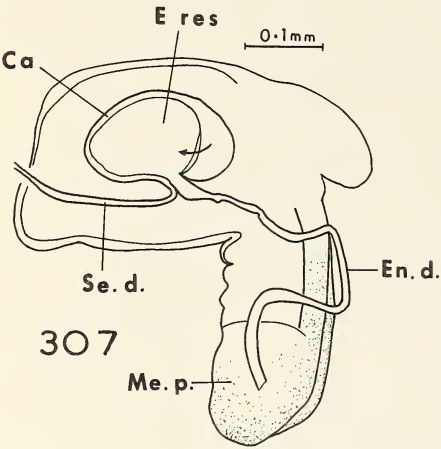
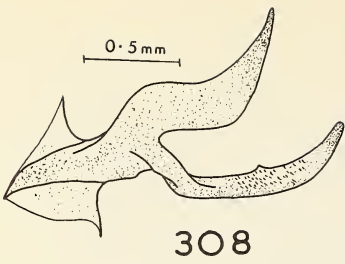
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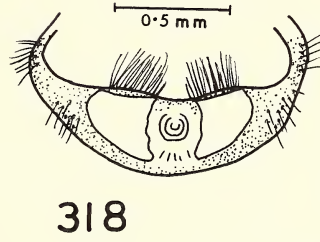
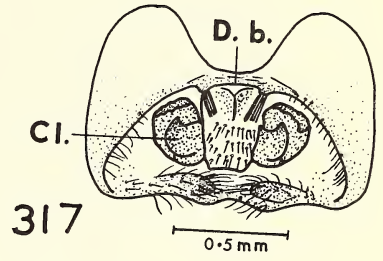
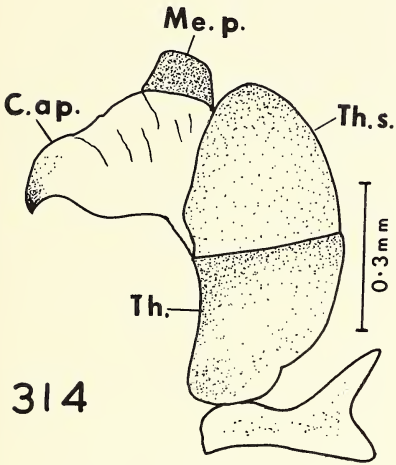
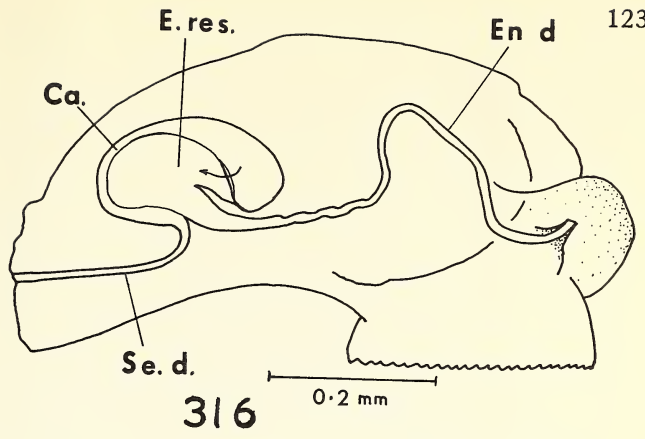
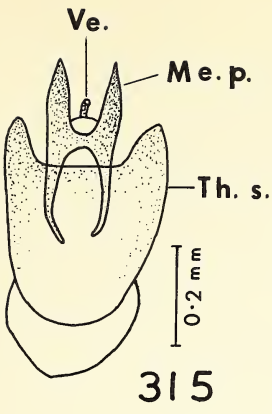




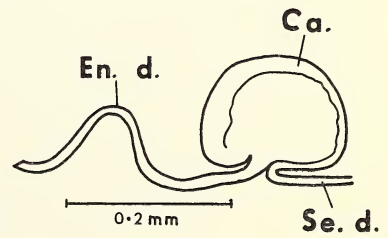
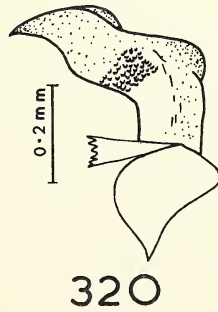
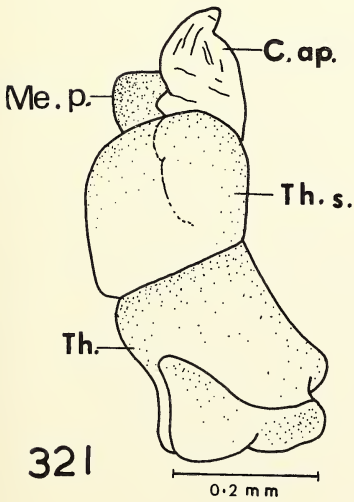
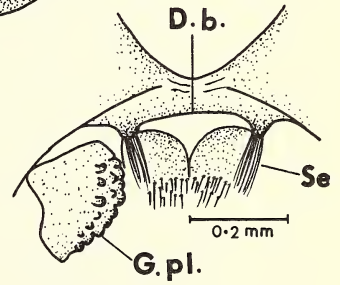




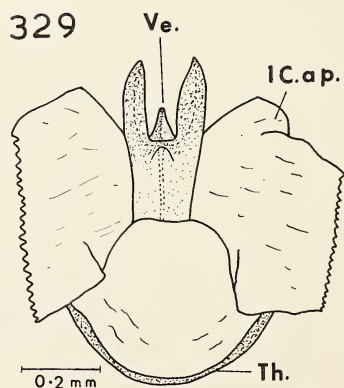
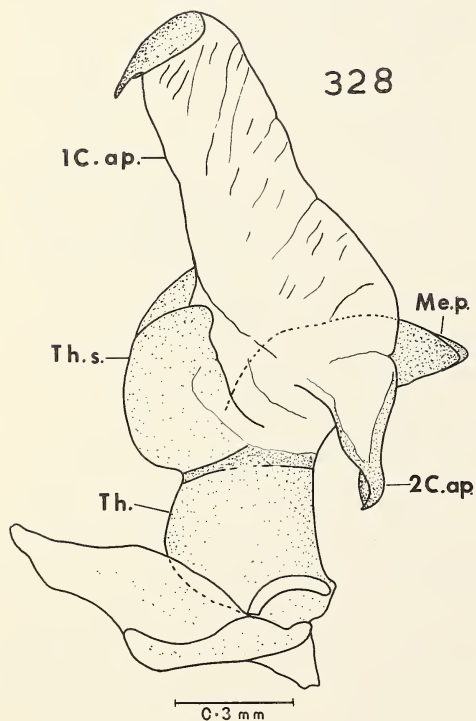
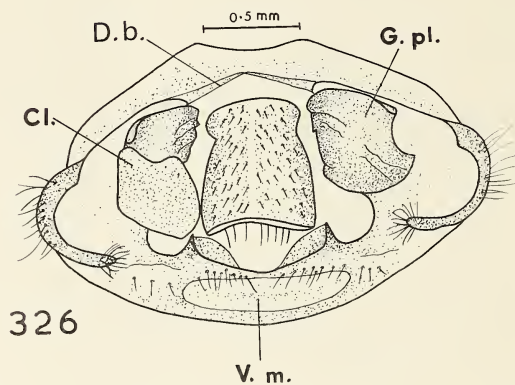
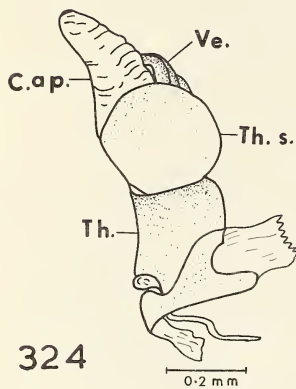
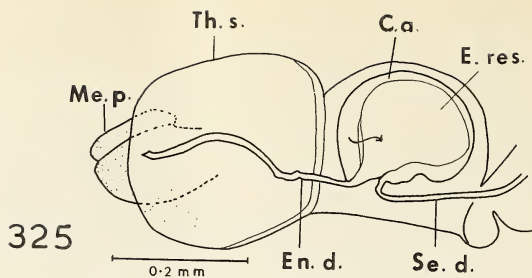
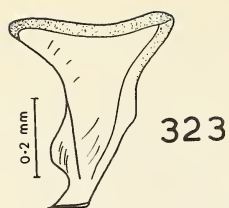


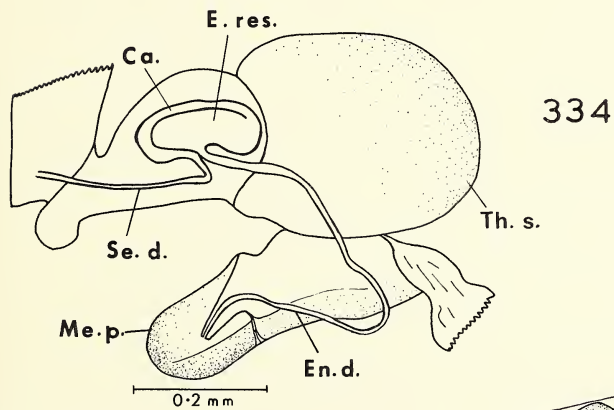
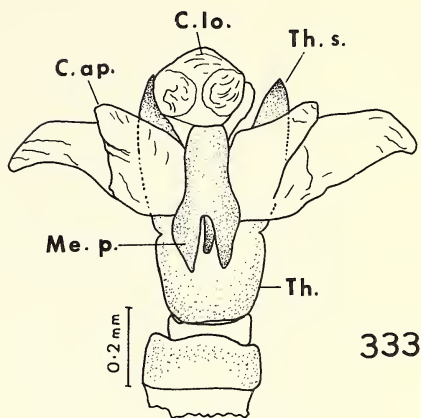
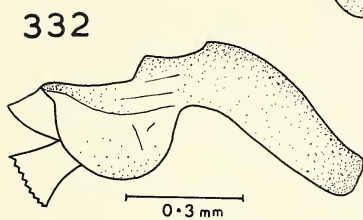
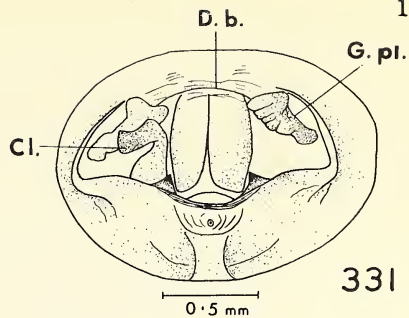
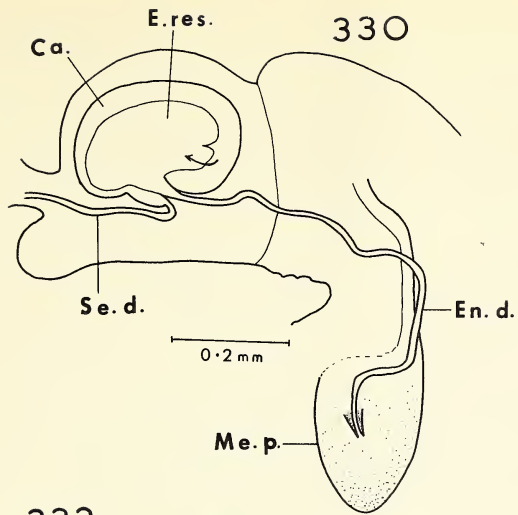


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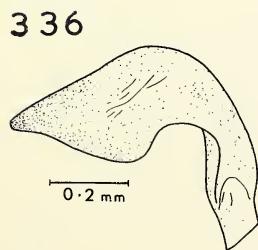
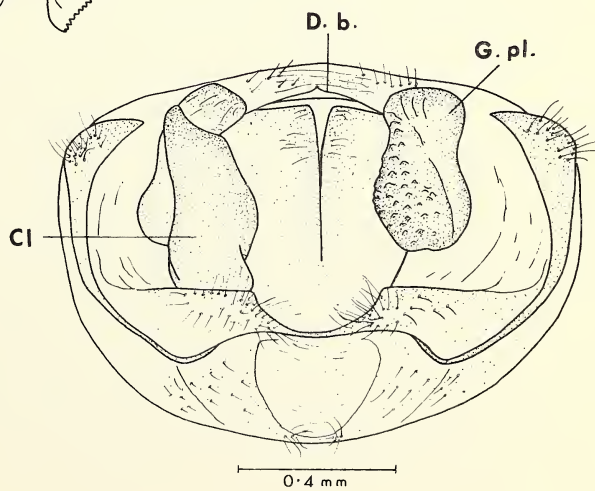


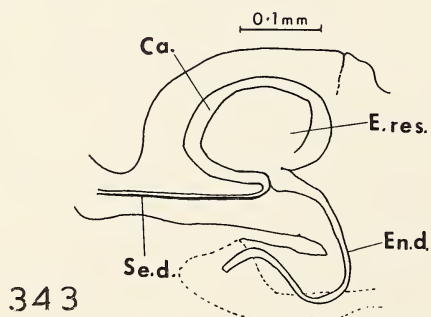
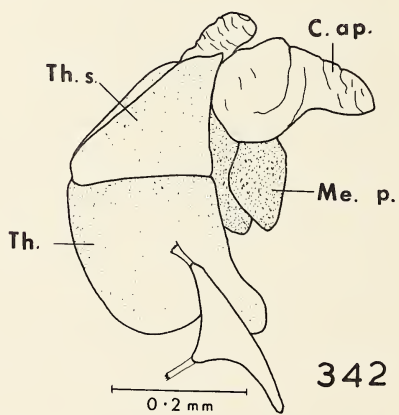
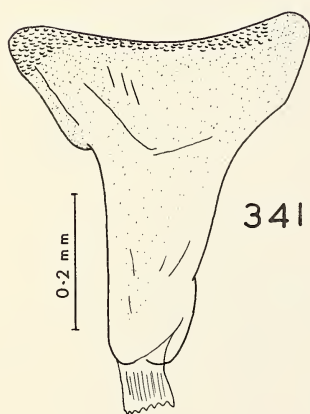
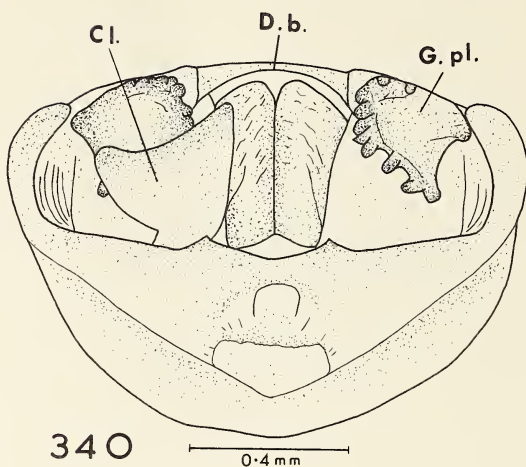
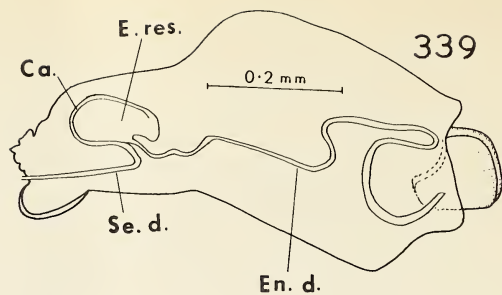
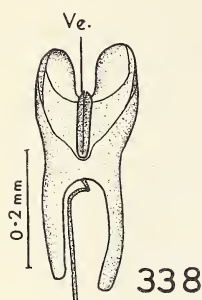
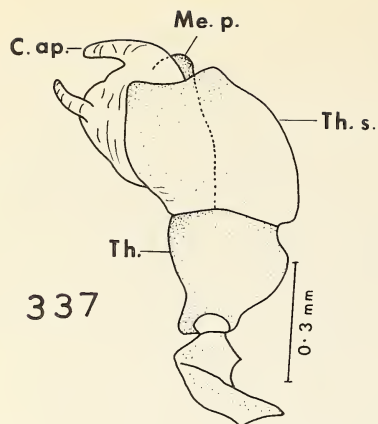


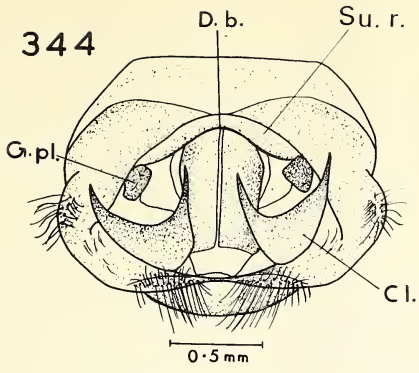




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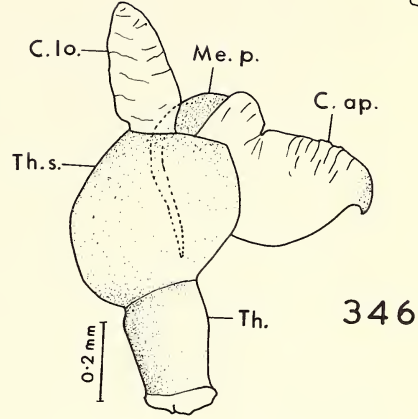
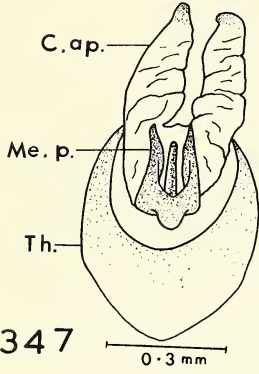




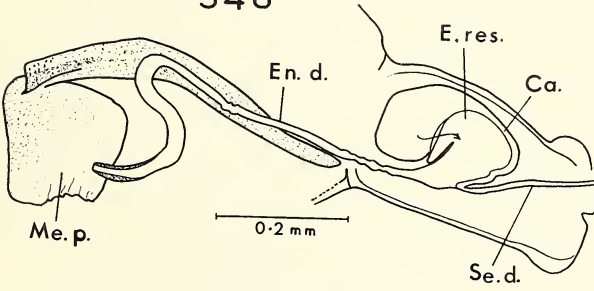


345

0.3 mm

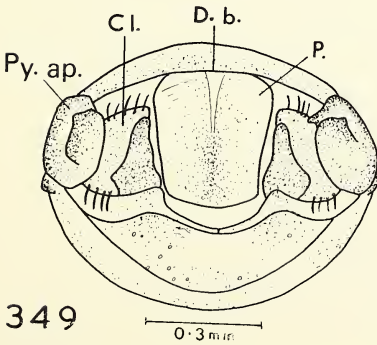


348



350

0.2 mm



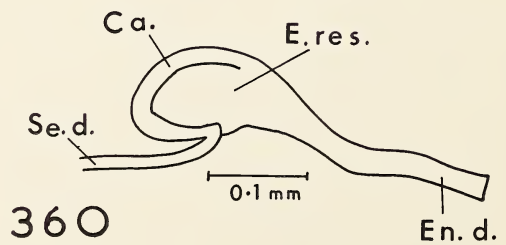
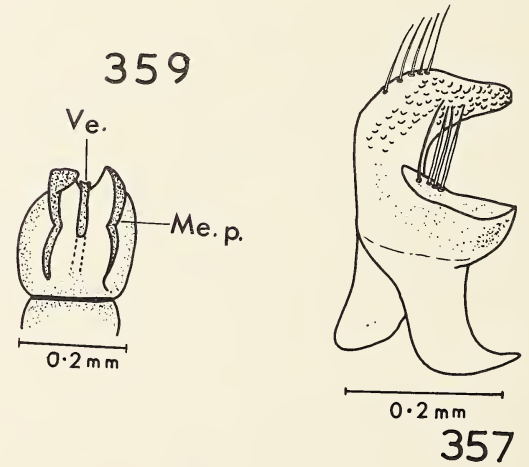
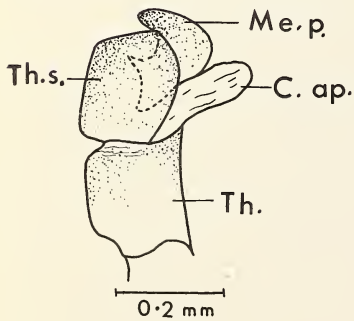
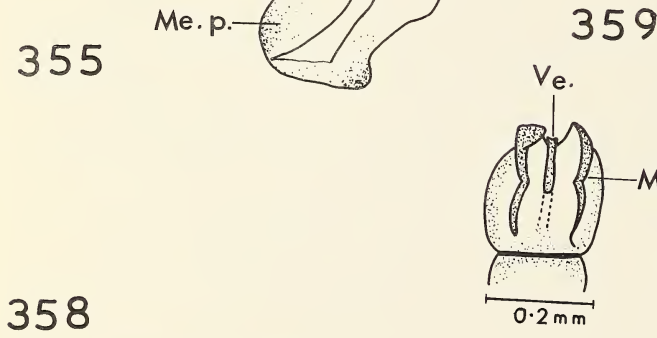
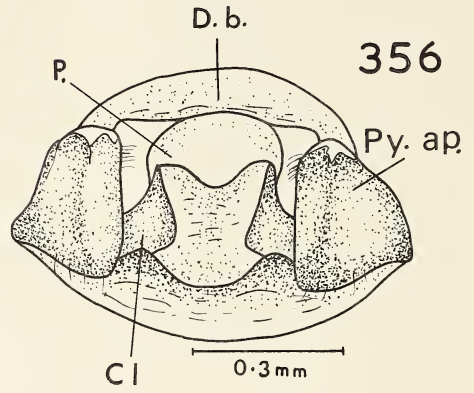
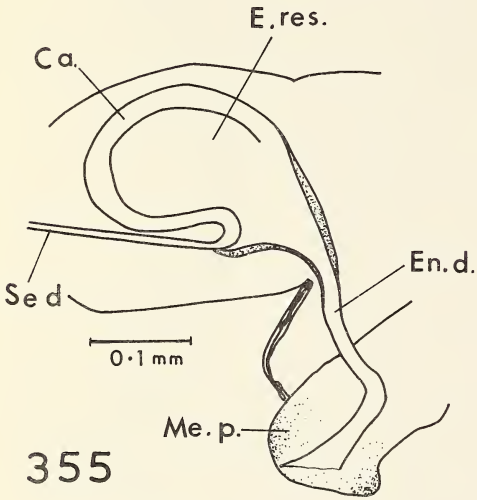
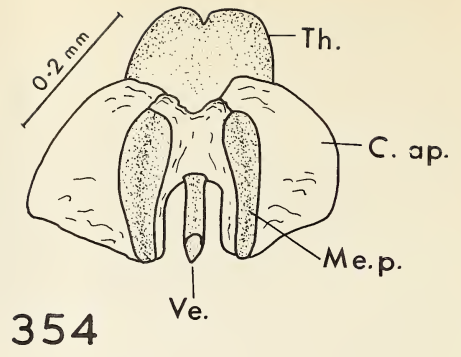
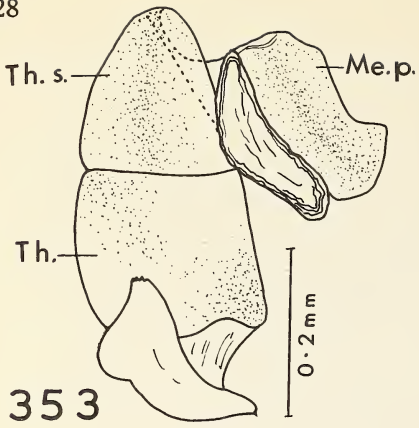
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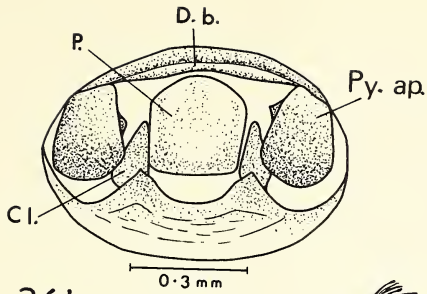
0.2 mm

352

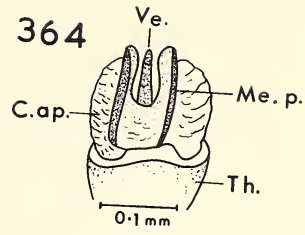
0.2 mm



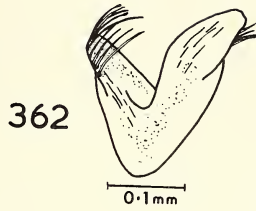




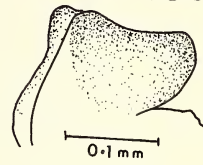
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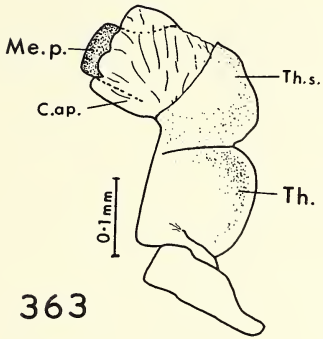
364



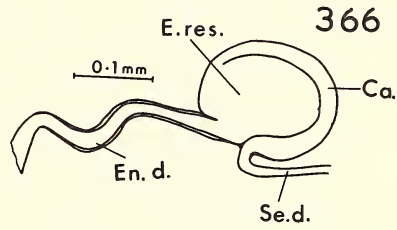
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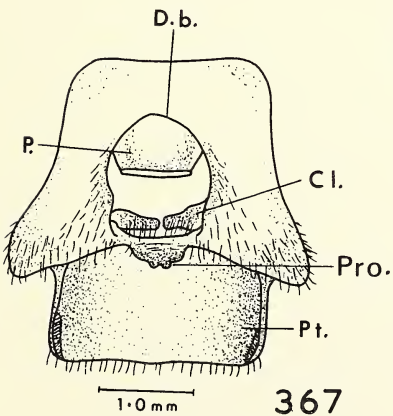
365



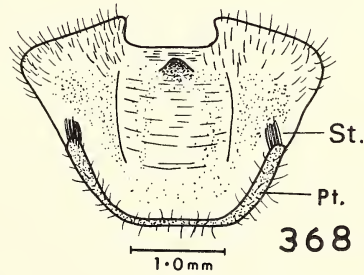
363



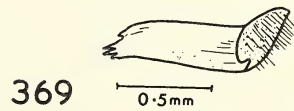
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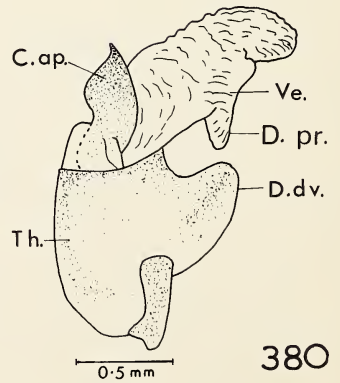
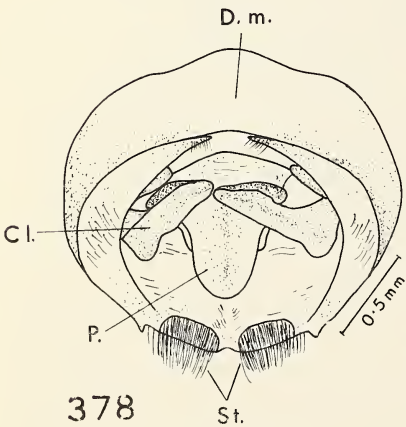
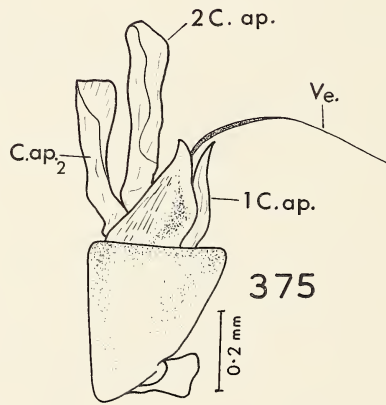
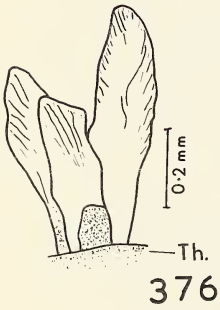
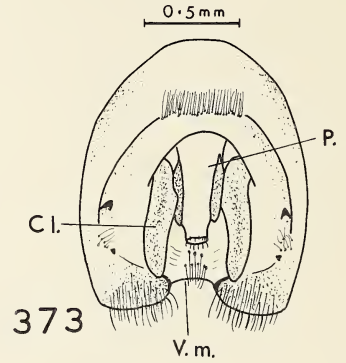
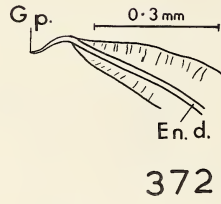
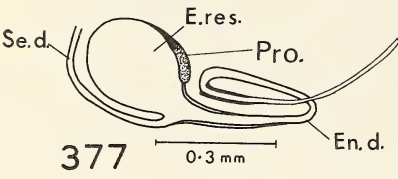
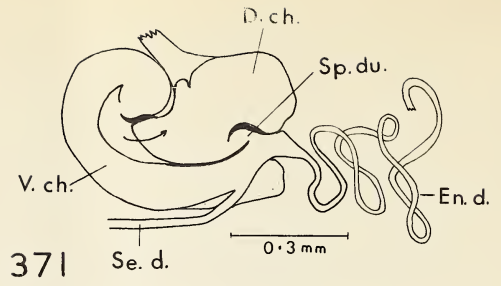
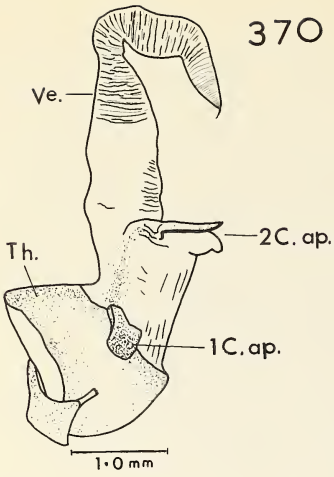
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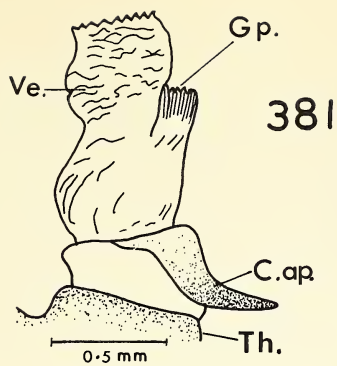


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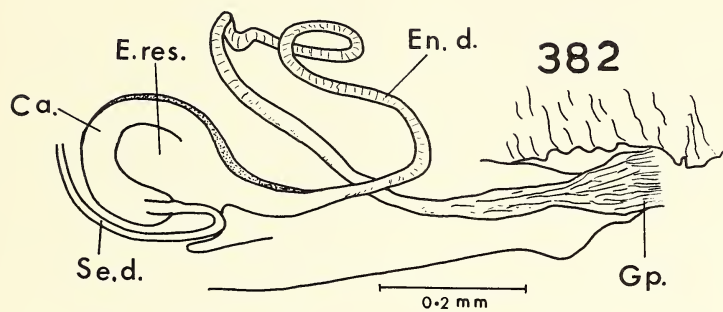
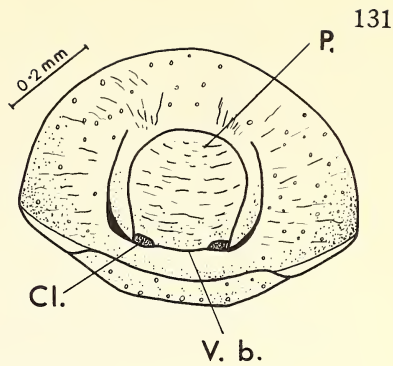


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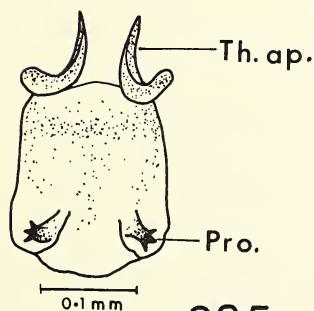




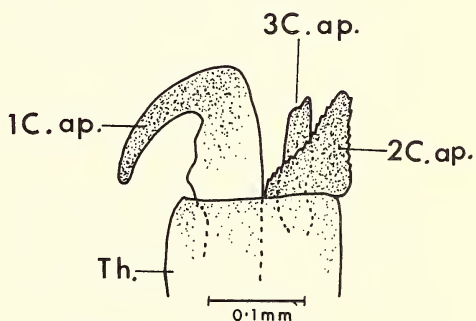
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384

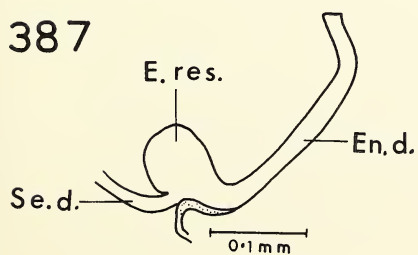


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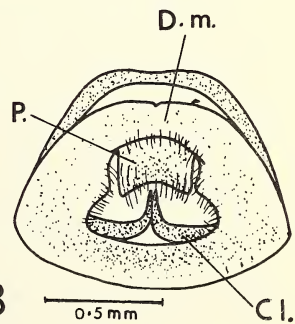


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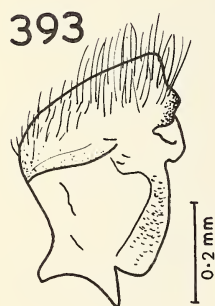
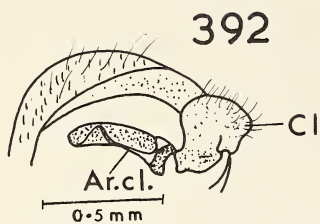
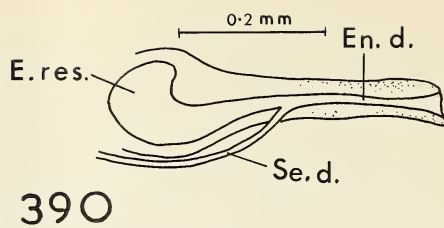
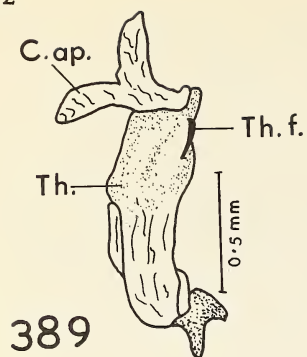
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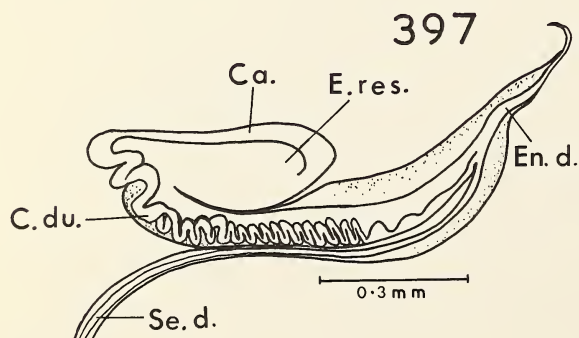
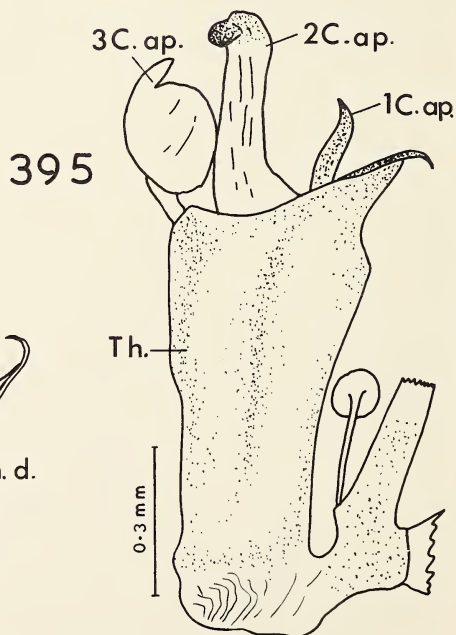
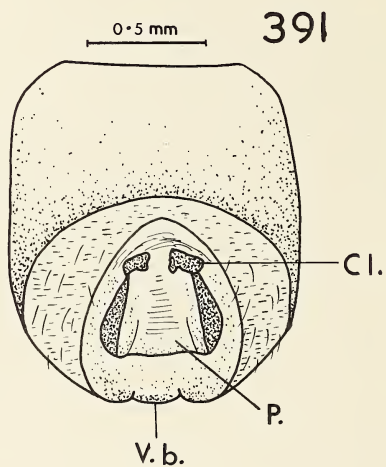
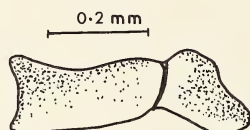
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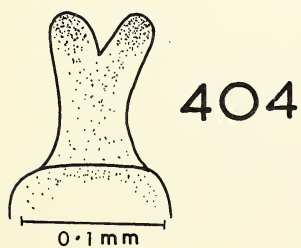
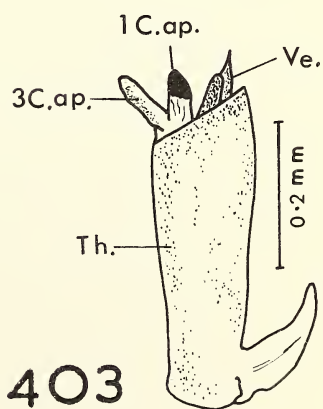
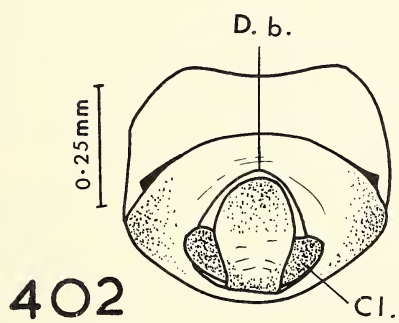
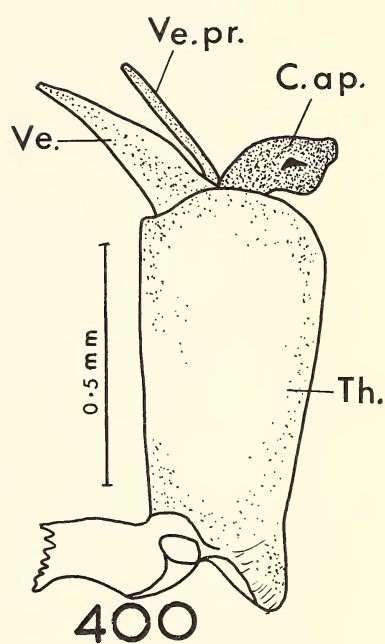
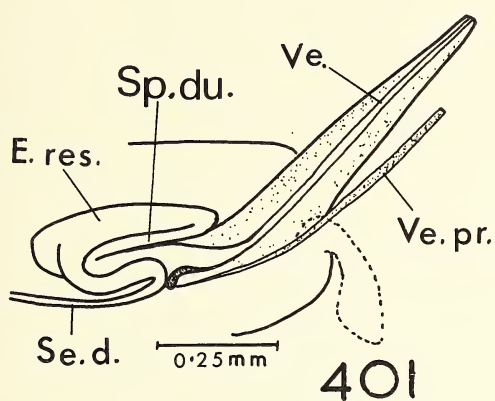
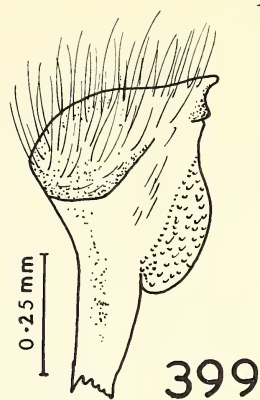
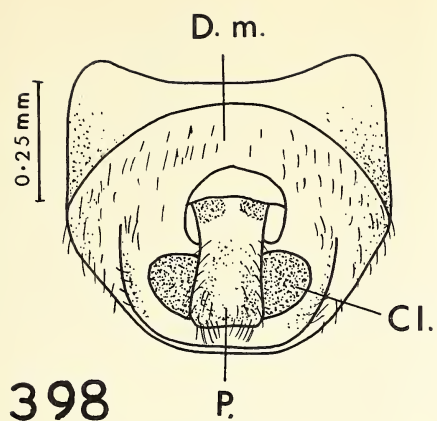


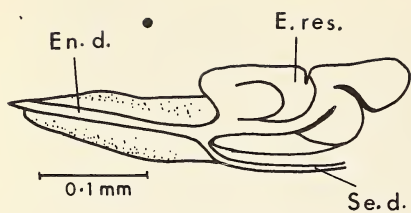




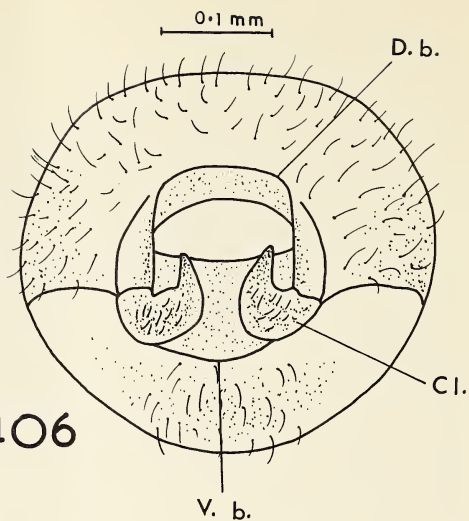
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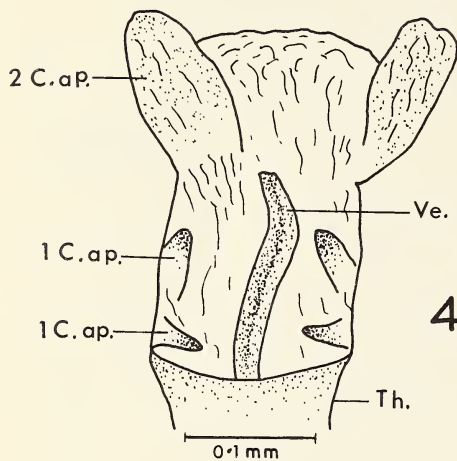




405



406

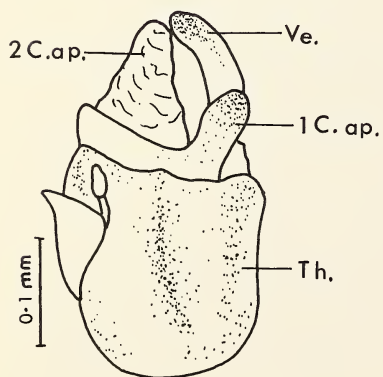


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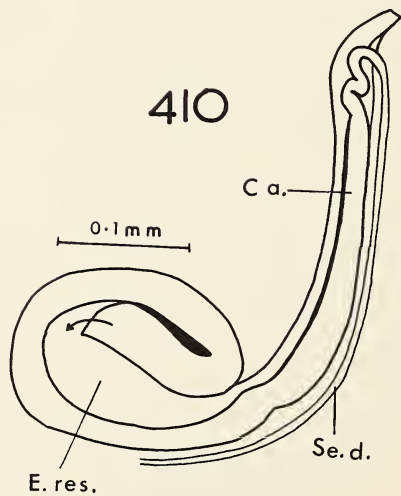


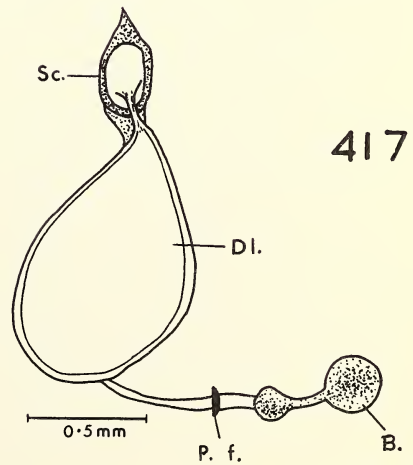
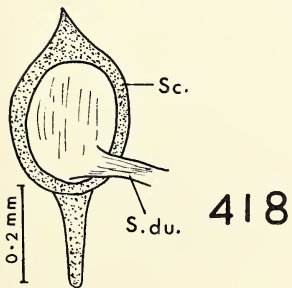
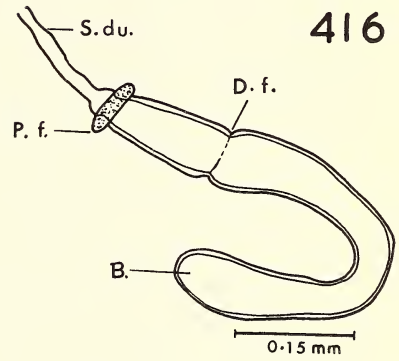
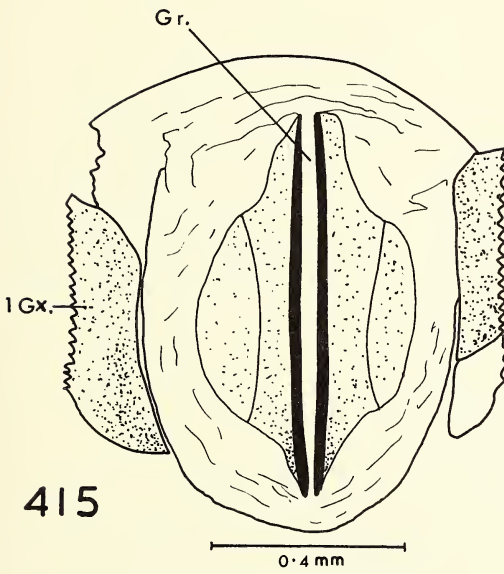
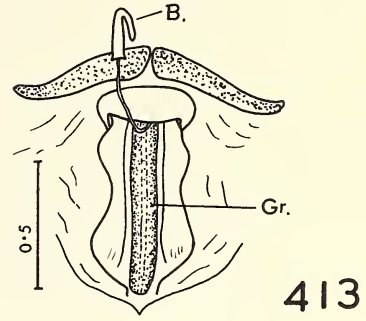
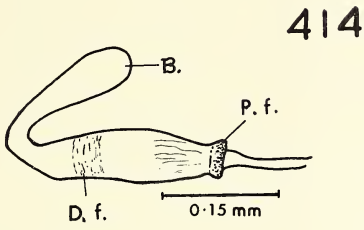
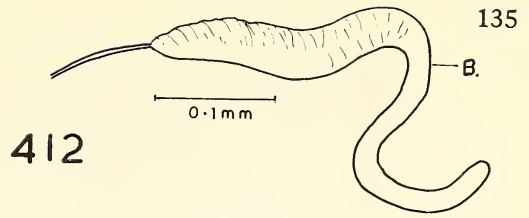
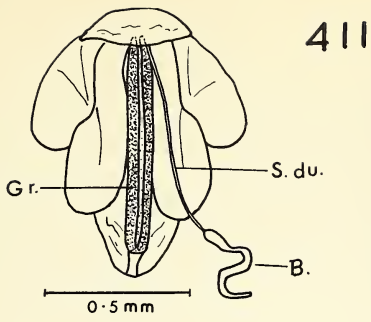
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408



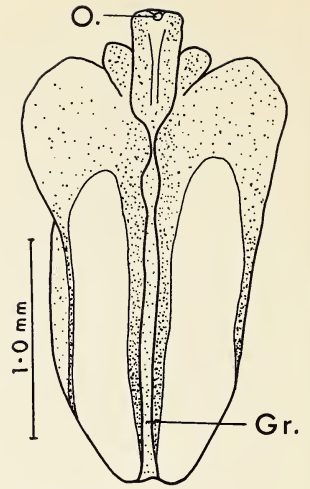
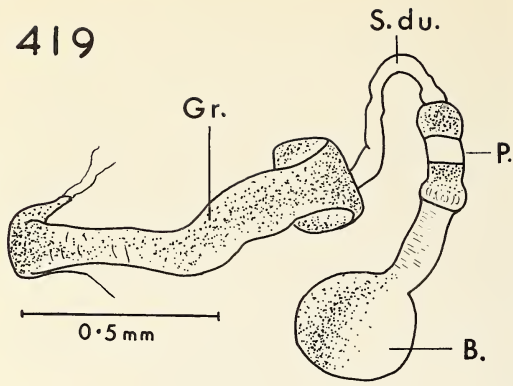
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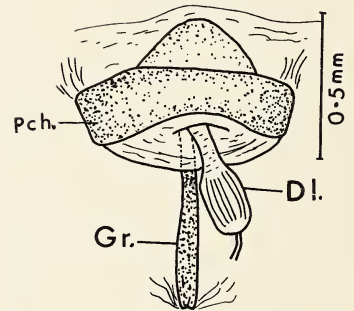
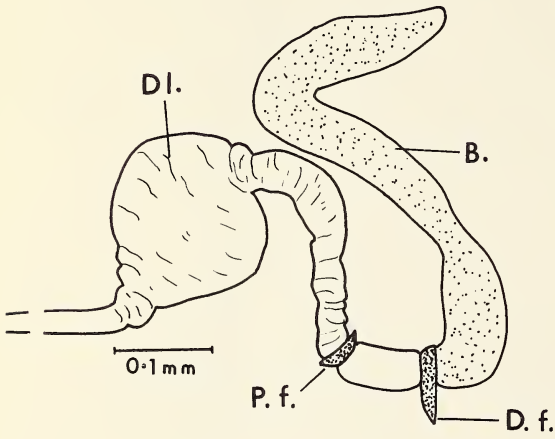


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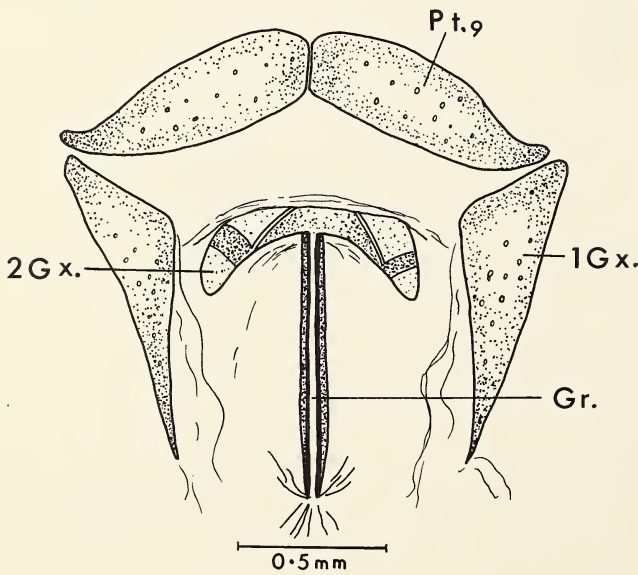


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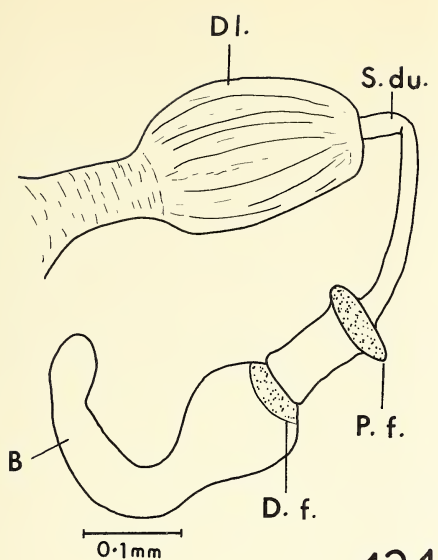
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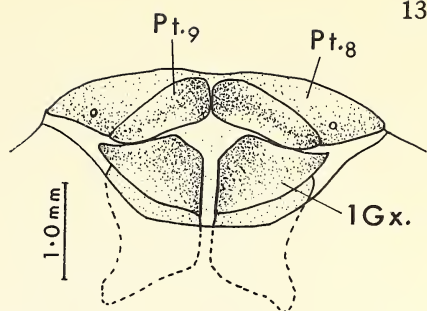
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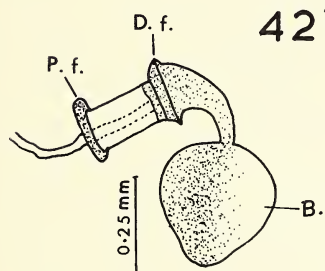
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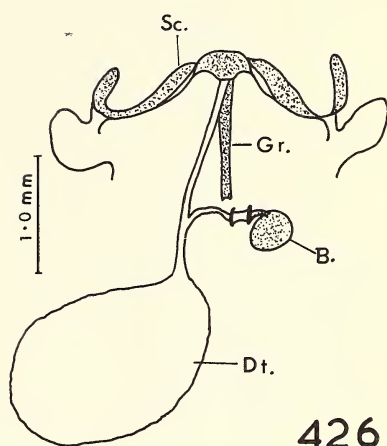
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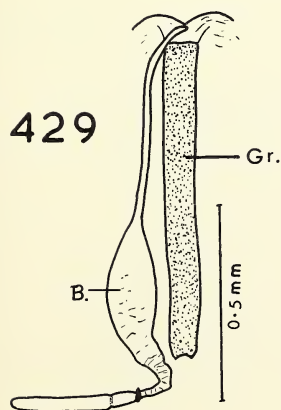
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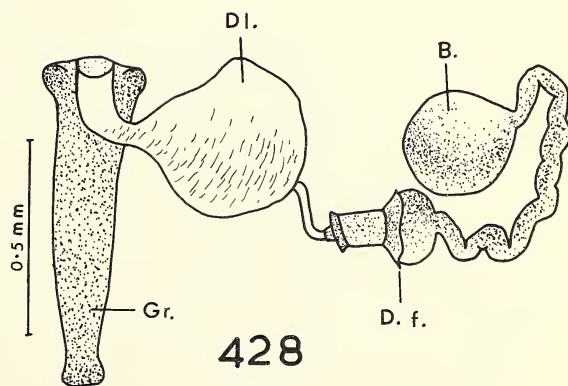
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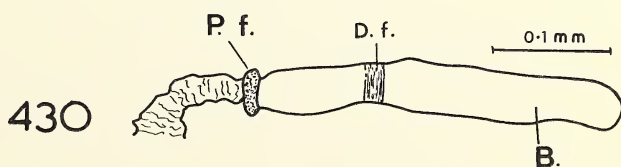
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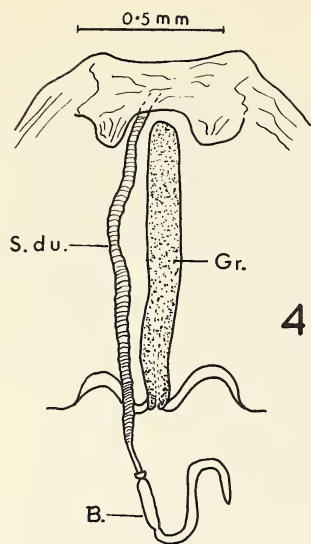
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428

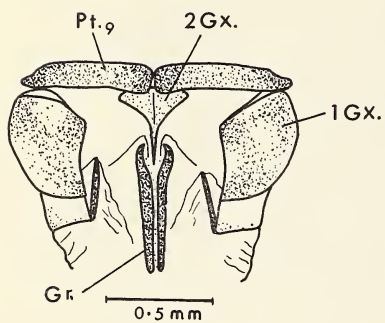
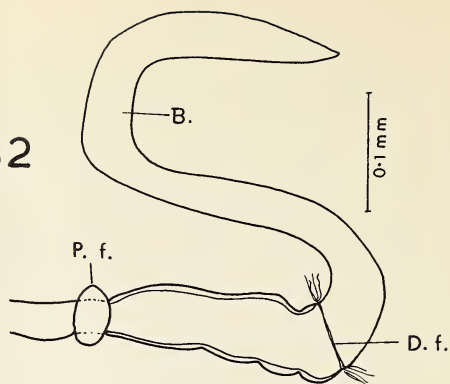


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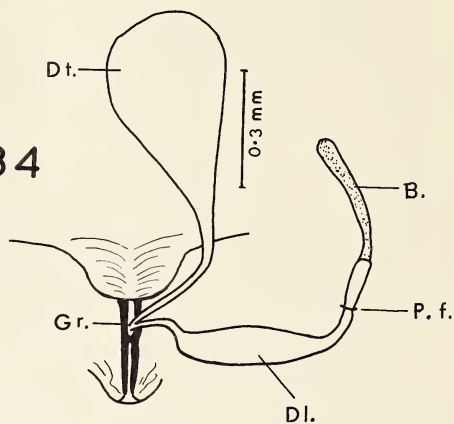
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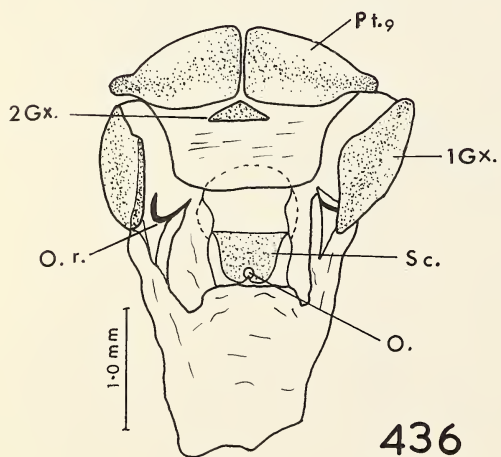
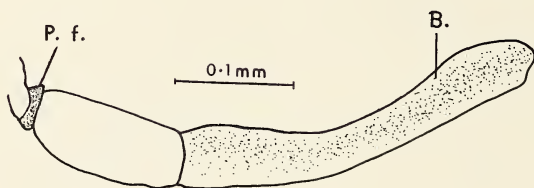


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434

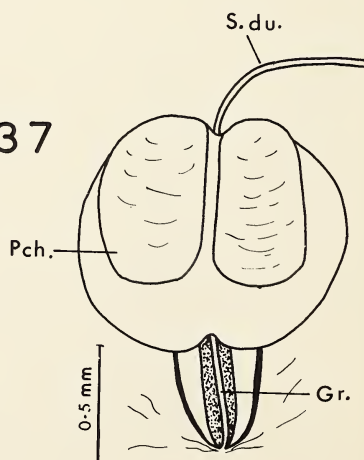


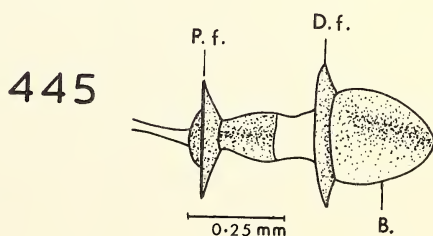
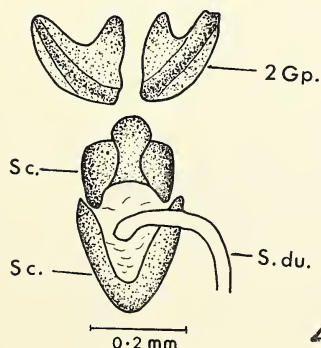
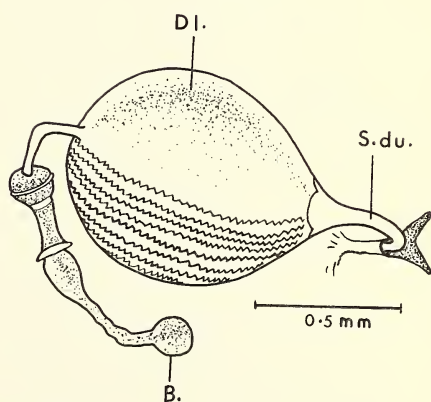
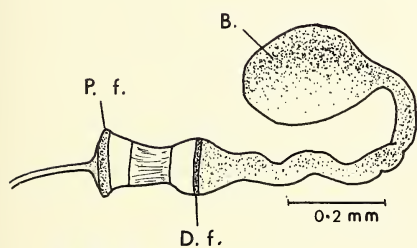
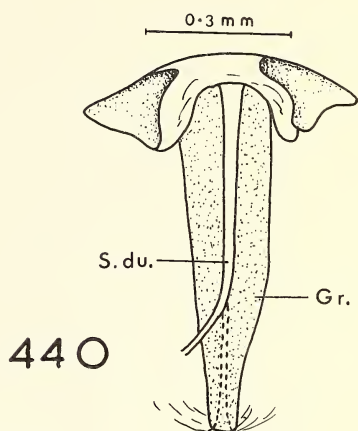
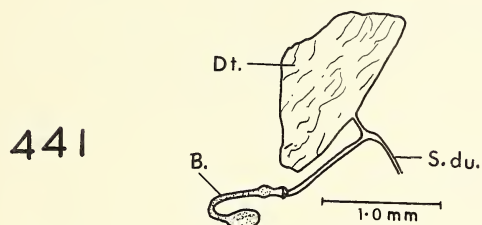
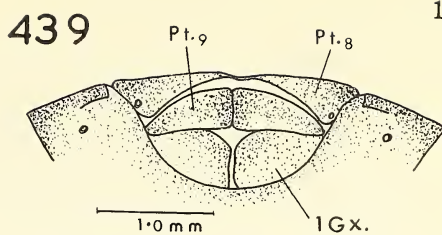
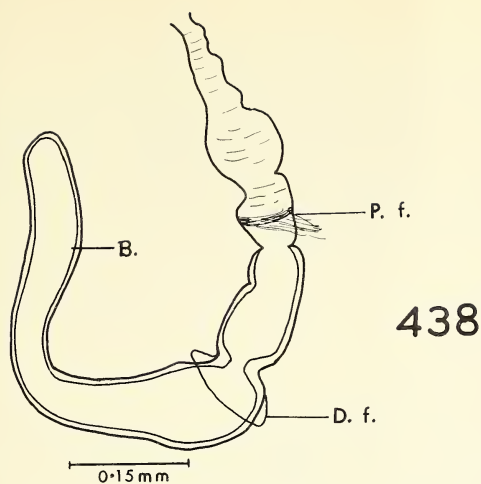
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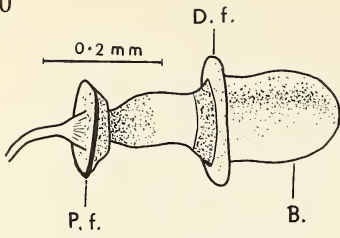
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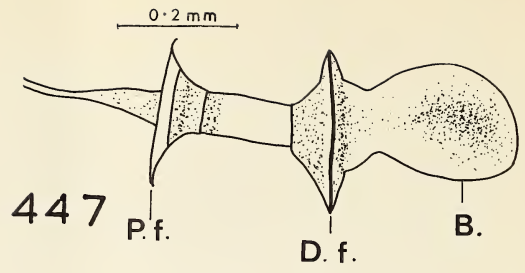




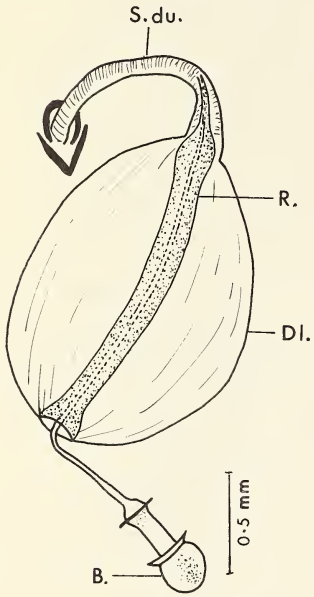




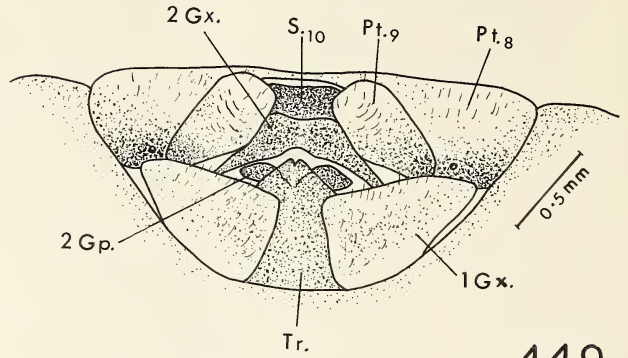
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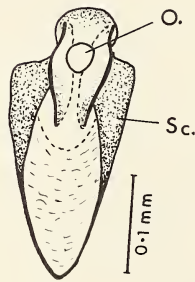
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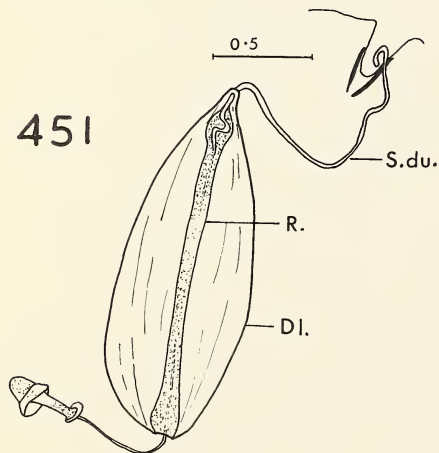
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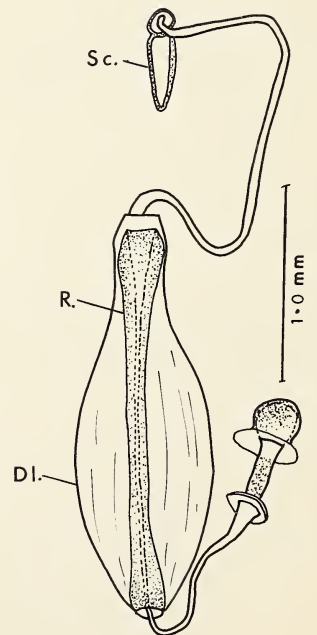
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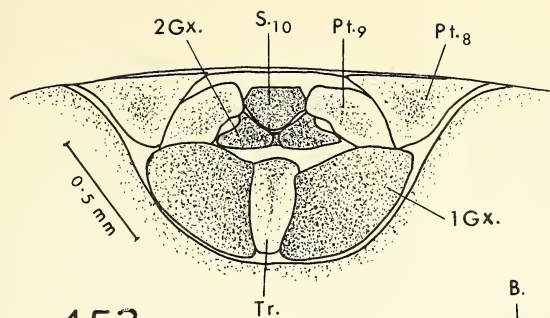
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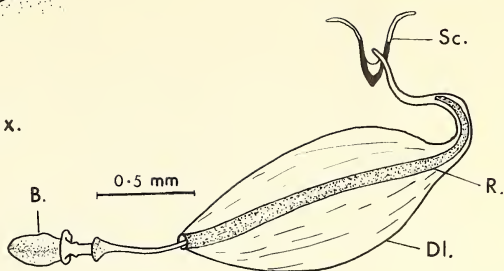
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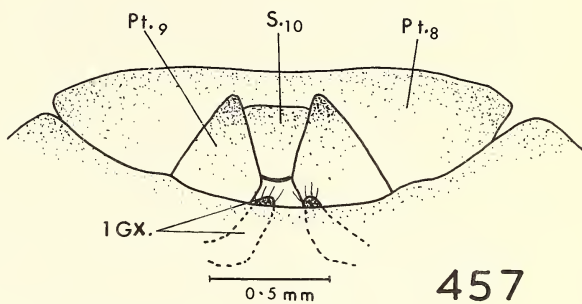
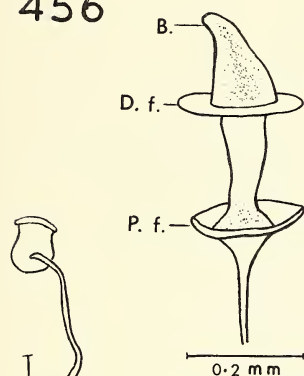


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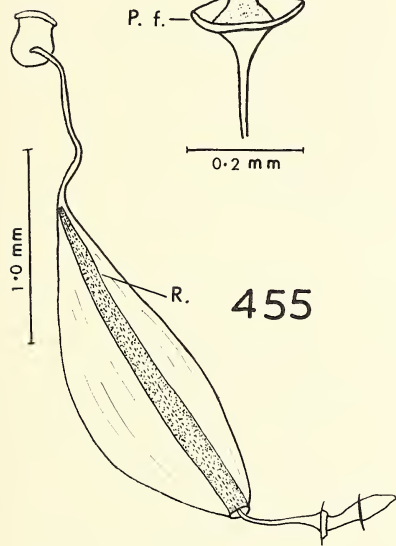


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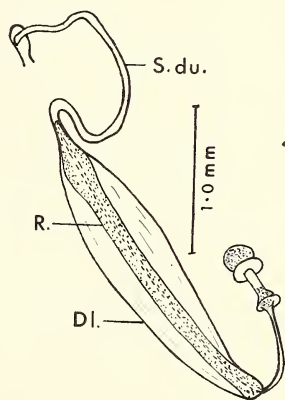
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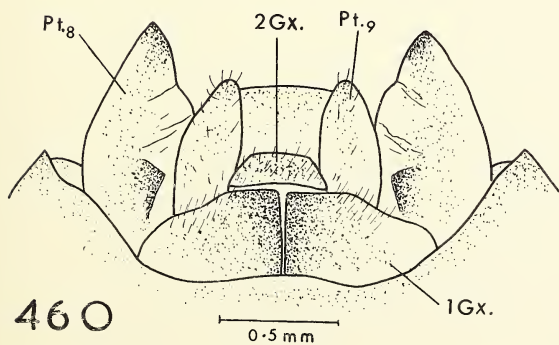
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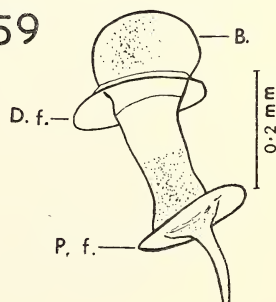


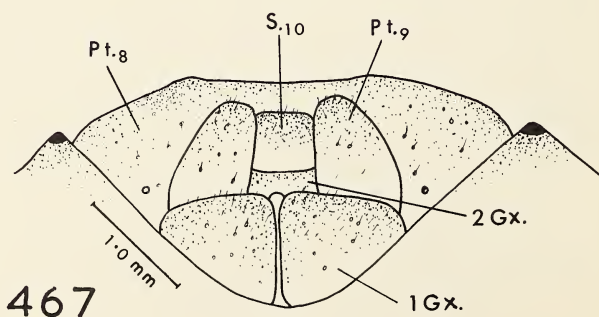
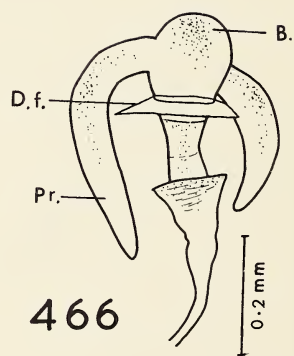
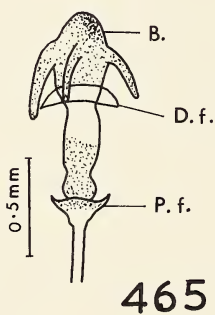
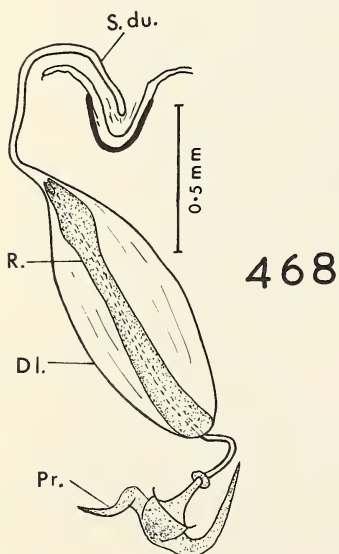
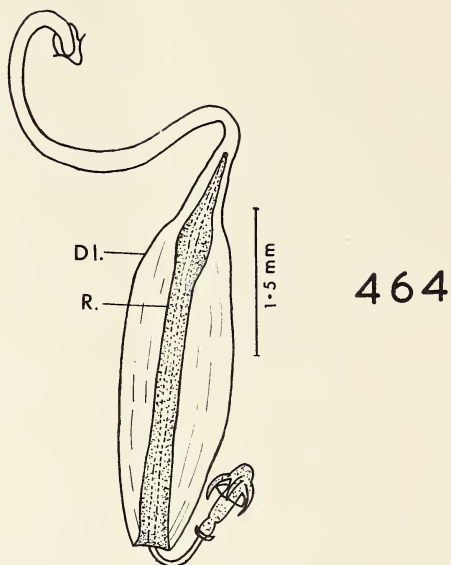
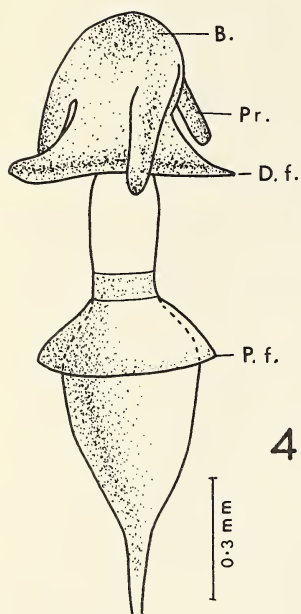
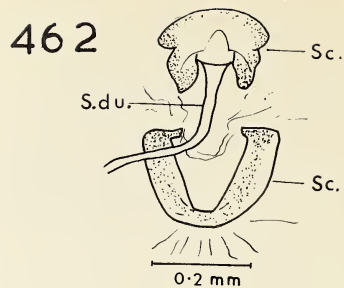
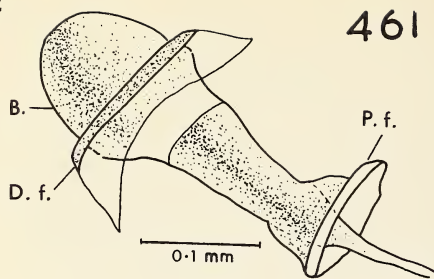
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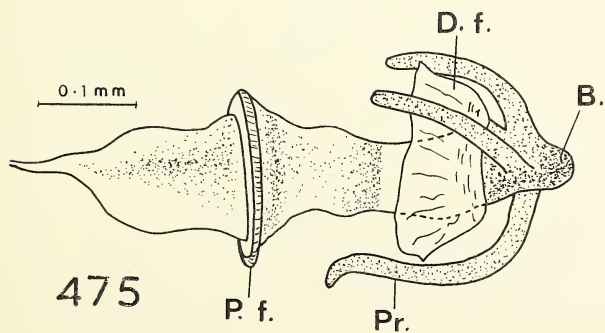
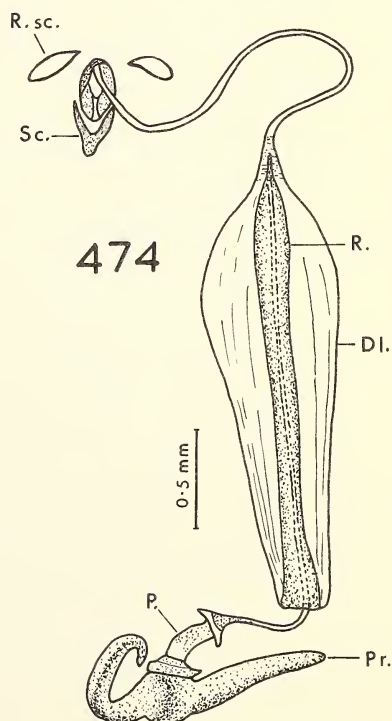
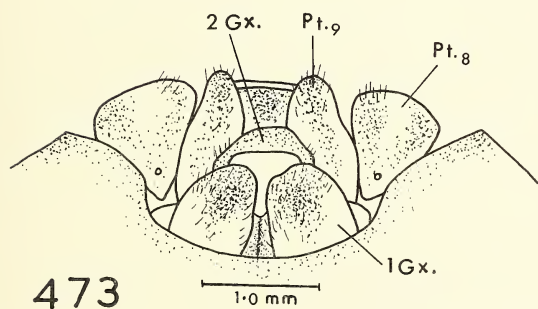
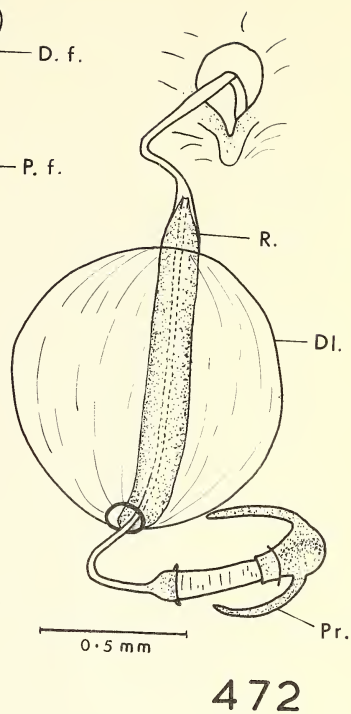
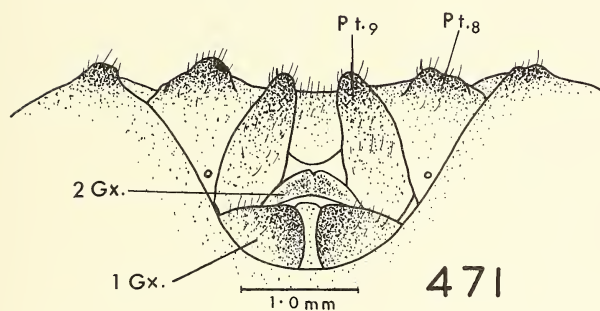
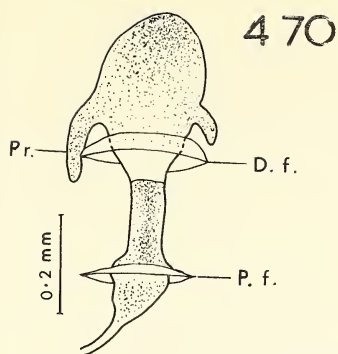
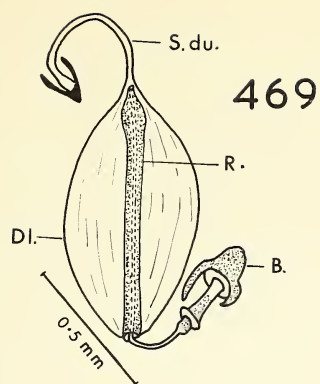


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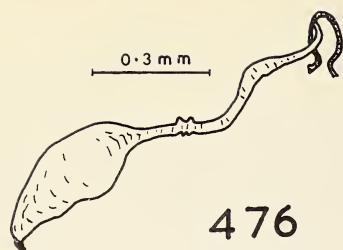
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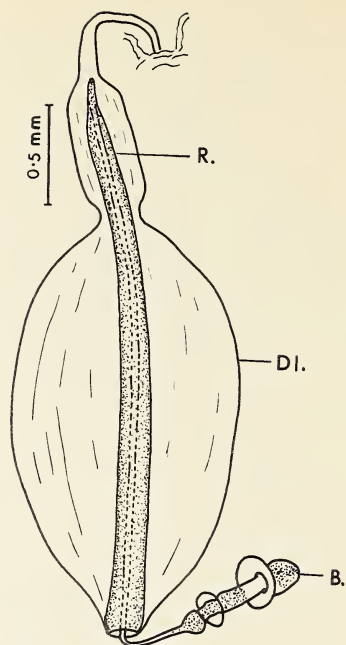






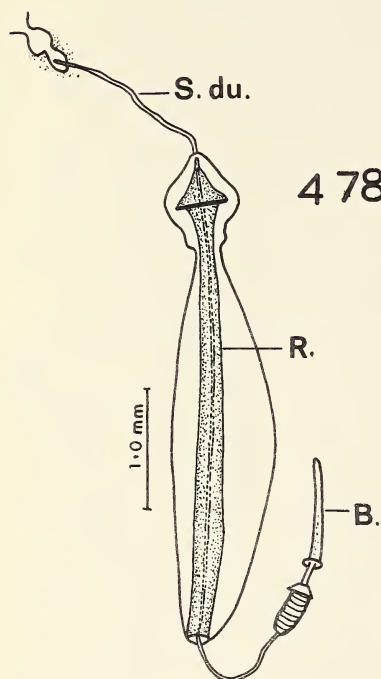


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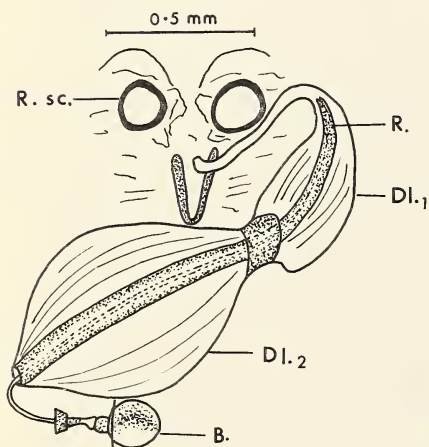
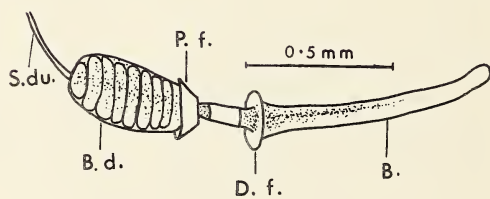


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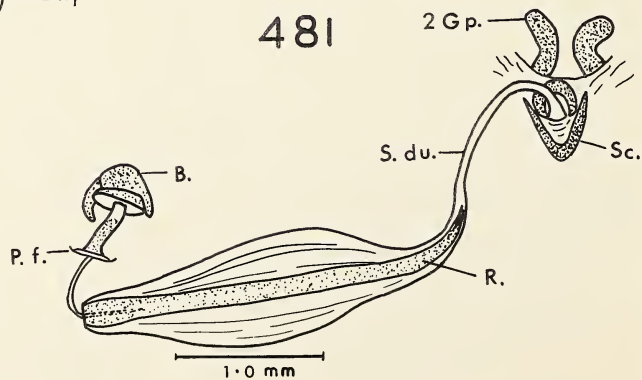
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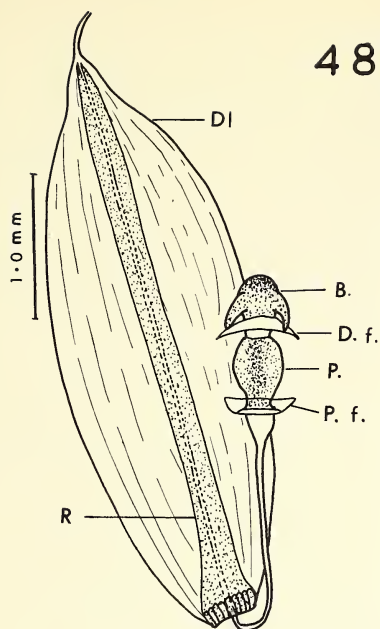


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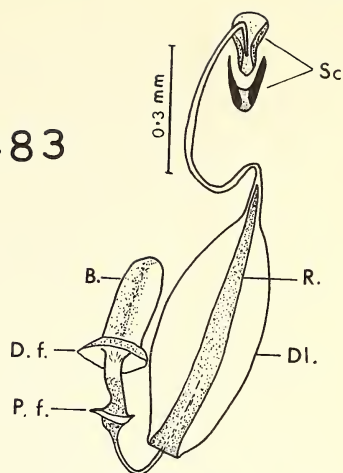


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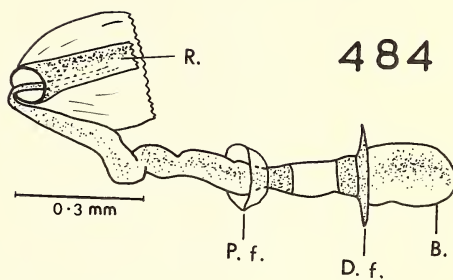
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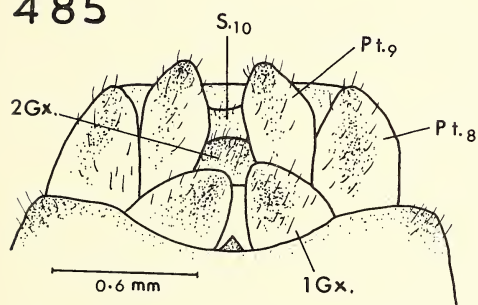
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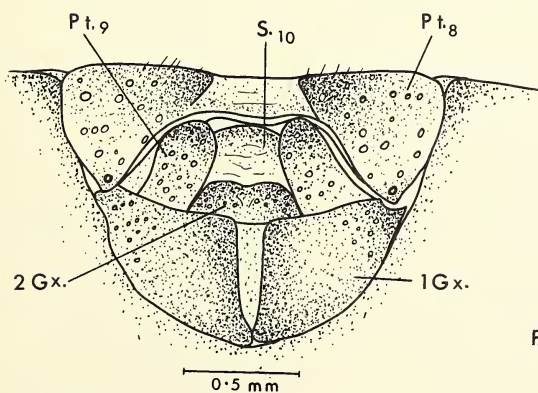
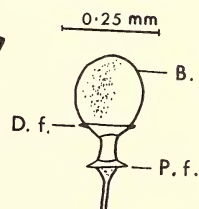
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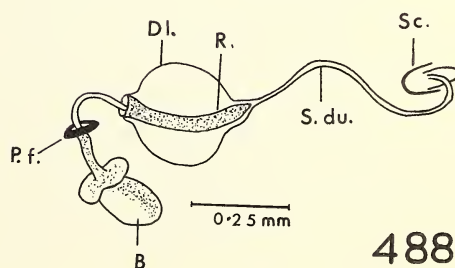
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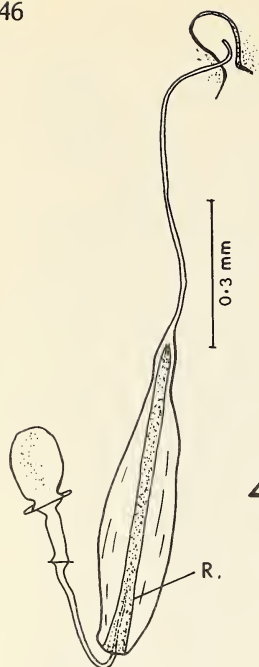
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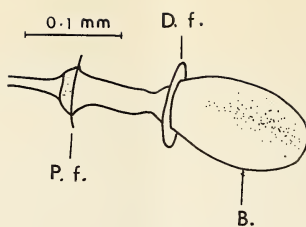
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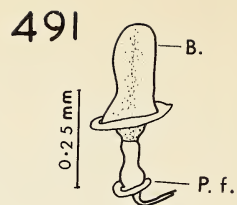
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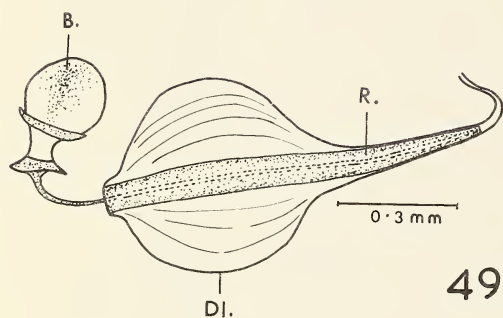
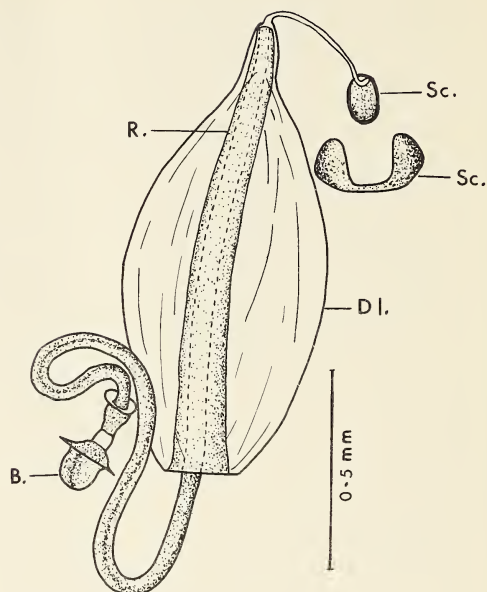


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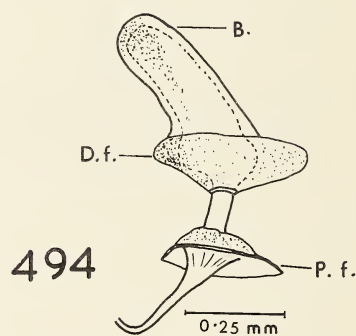


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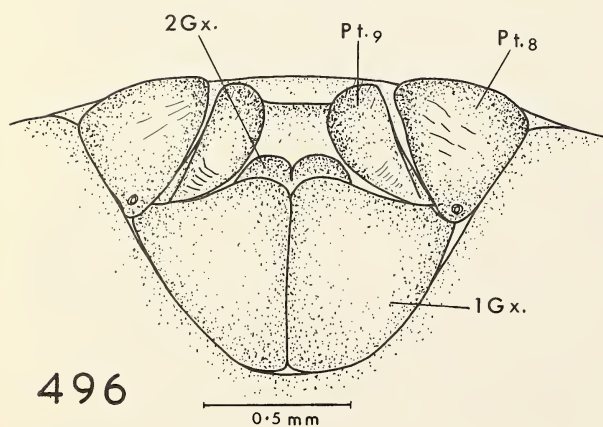
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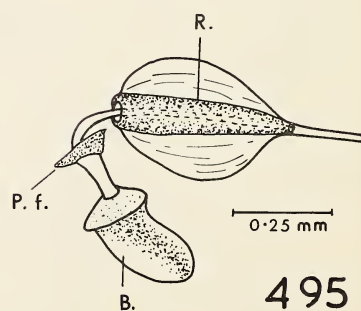
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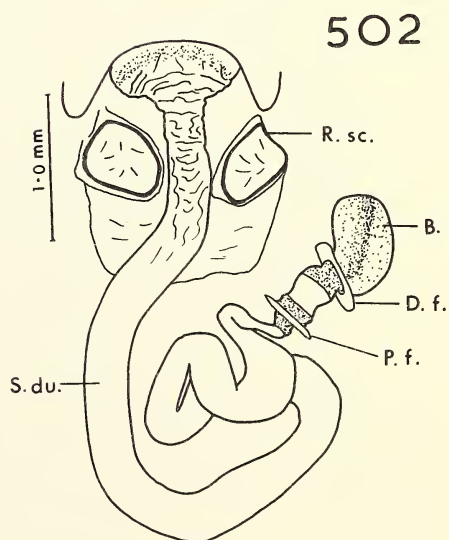
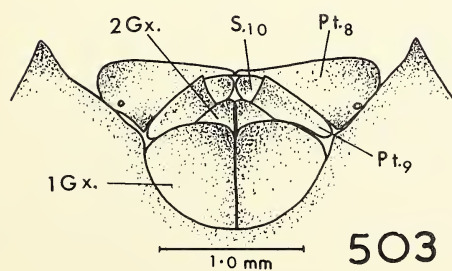
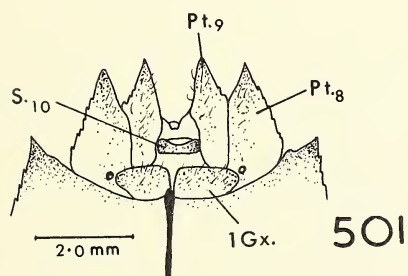
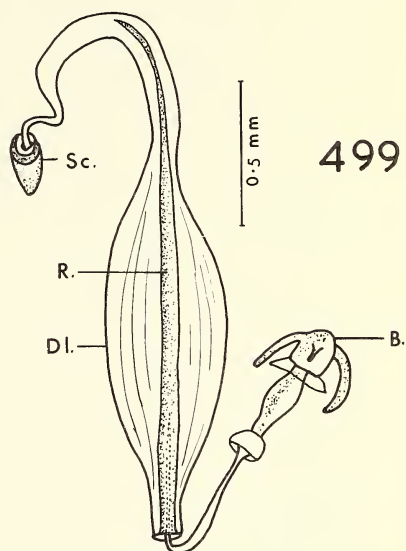
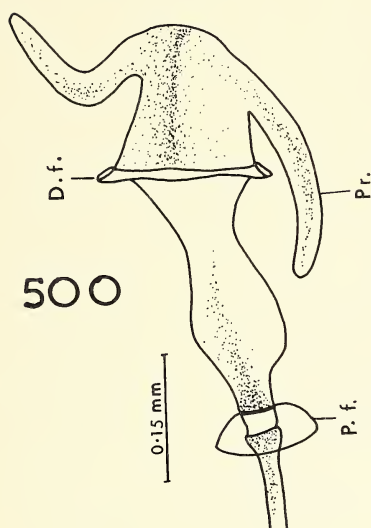
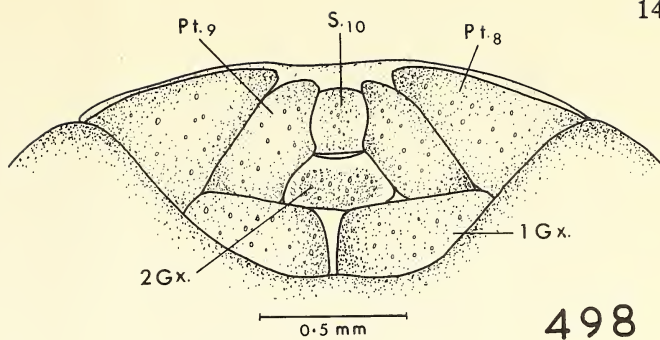
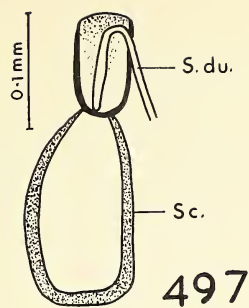
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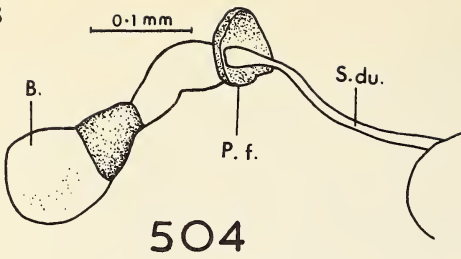
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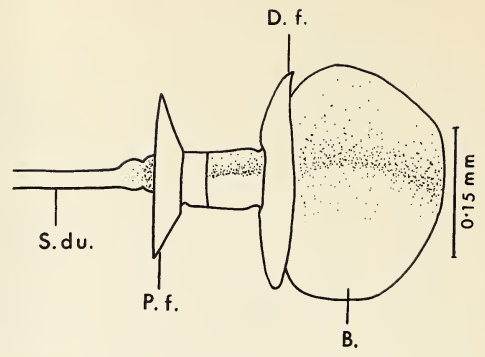
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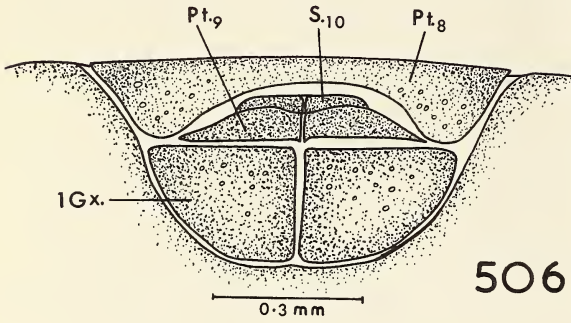




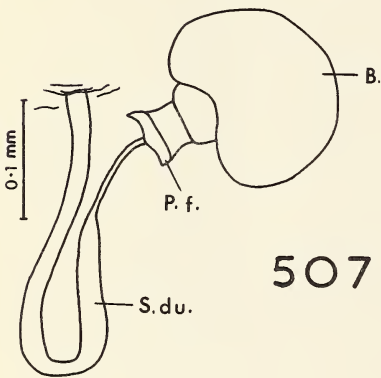
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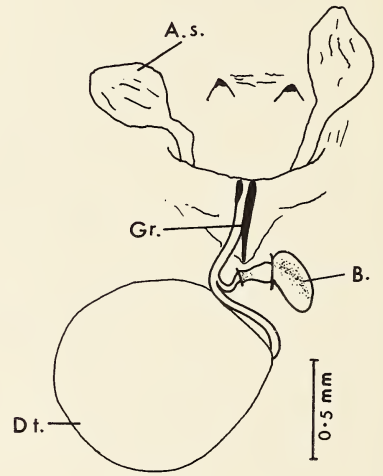
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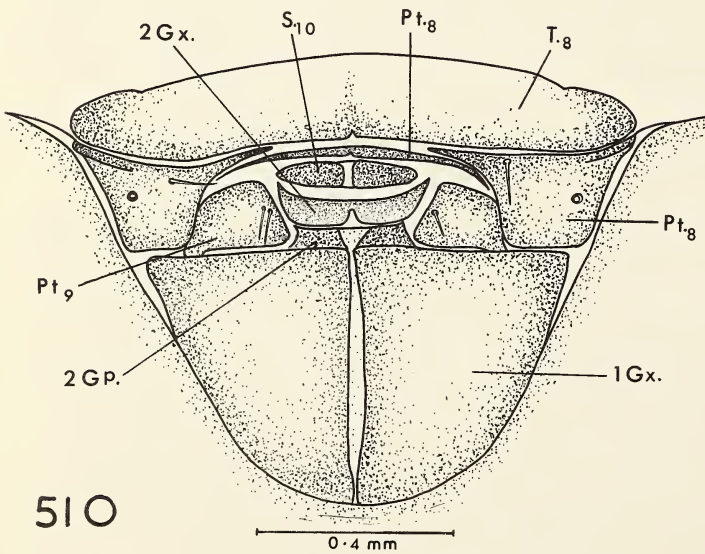
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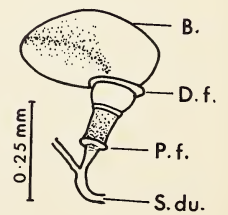
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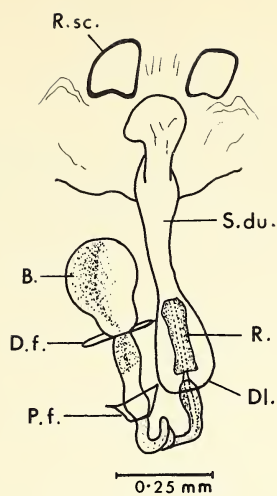
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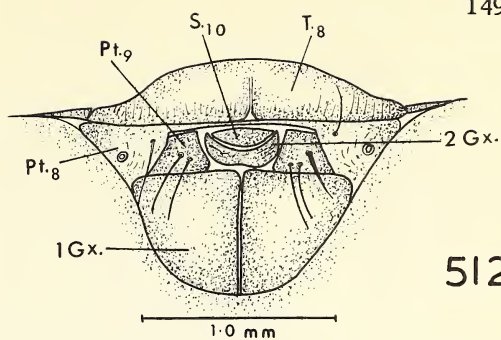
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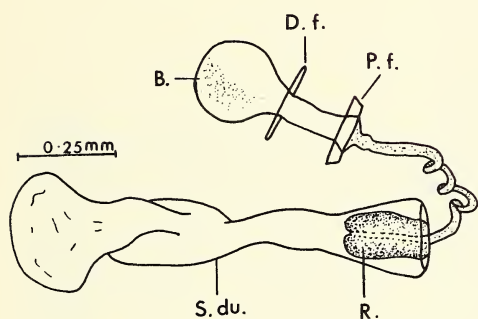
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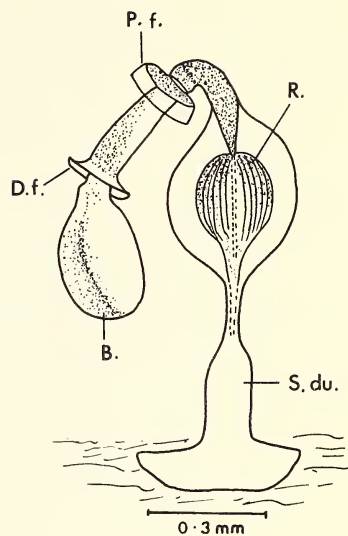
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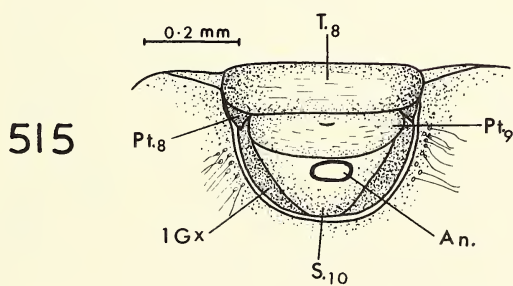
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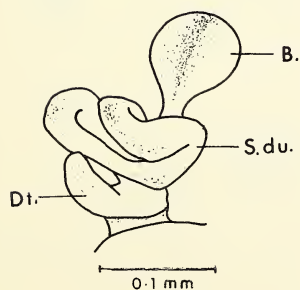
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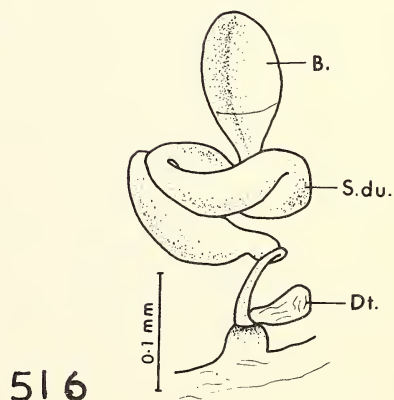
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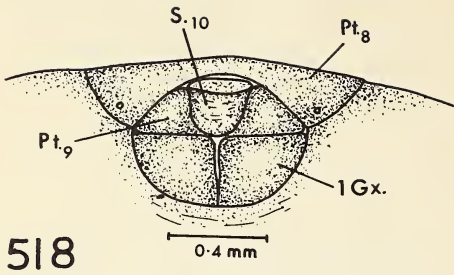
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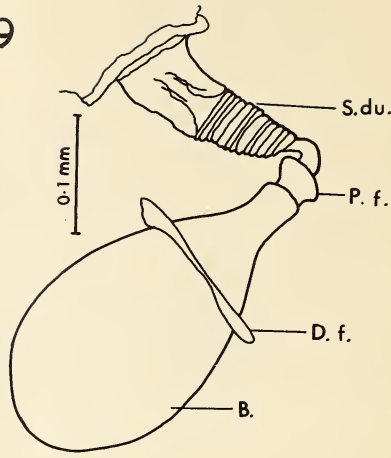
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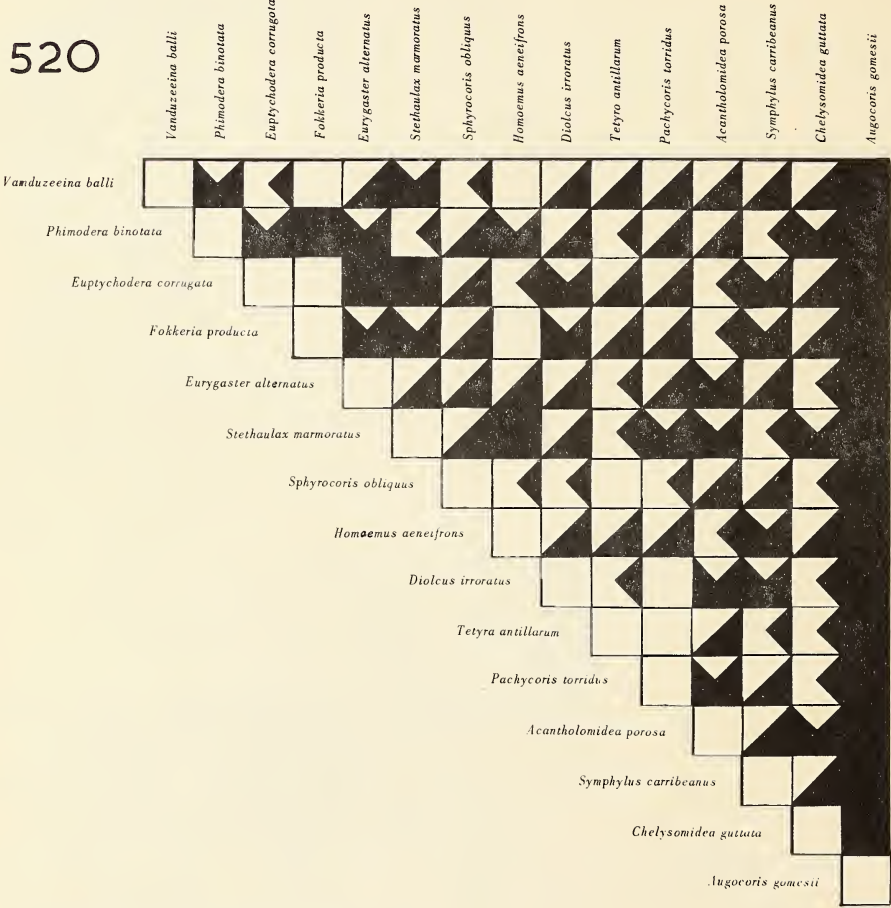
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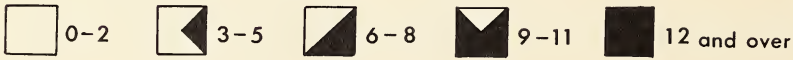
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# Quaestiones entomologicae

A periodical record of entomological investigations,  
published at the Department of Entomology, Uni-  
versity of Alberta, Edmonton, Canada.



VOLUME II

NUMBER 2

APRIL 1966





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Number 2

6 April 1966

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## Editorial — An eye for an I

Eye, not "the author", "the writer", or any other circumlocutory description of myself, but eye, Brian Hocking, am publicly and without shame pleading for the return of the first person, in all cases, singular and plural, to its modest but respectable position in scientific literature. This group of words provides the very brevity and precision that the present-day world needs. To outlaw the whole of the first person simply because some people have found difficulty in the discreet use of the nominative singular is, like total abstinence, an admission of weakness. More than that, this false modesty must have cost the printing presses of the world many millions of extra words over the last few years. Can they or the reading public spare the time?

How delightfully simple this is, this eye that we shun so scrupulously. Just one letter, and the simplest one at that. Just a line. Yet surely this is the most precise line in the language; no possible ambiguity here. It can mean only one thing. What about our alternative "the author"? It is ten times as long for a start. In some scientific papers many authors are referred to so that it becomes necessary to define him further as "the present author". So many times does "the present author" appear in some papers that eye come to regard him as the ever-present author. Although his personality is rarely present, he is far more conspicuous and demanding than if he were just an eye.

English has got along for some time now without its second person singular, although eye for one would welcome the return of the outspoken "Where art thou?" and "Thou shalt not". The use of the plural form is usually, after all, a false politeness, just as avoiding the eye is a false modesty. If we are not to have all of our first persons restored, where is it to end? And what have we left? Already nothing but second- and third-rate personal pronouns. And there appears to be no authority for all this; eye suspect an editorial conspiracy. This is what the authorities say:-

Perrin: "I can be used wherever it is needed. People with only average concern for themselves need not worry; the conceited will give themselves away anyway. Circumlocutions to get around the natural use of I are usually awkward and likely to attract attention to themselves." (p. 599)

Quiller - Couch: "... when man asks questions about his fortune or destiny he asks them most effectively in the first person." (p. 141)

Gowers: "Official prose is made unnecessarily ugly by a shyness of pronouns." (p. 74)

The only support eye can find for the outlawing of the first person is in the Royal Society publication "General Notes on the Preparation of Scientific Papers". It says, referring only to a synopsis (p. 24): "It is preferable to use the third person", but elsewhere (p. 2): "It may seem superfluous to state that the paper should be clear, precise, logical and brief... Experience shows that clarity and precision are best achieved by the use of short words and simple sentences." Eye can find no comments by Anderson and Thistle, or in The Canadian Government Editorial Style Manual.

The last stronghold of the first person was for some time the acknowledgment section of papers; here the occasional I and we still linger on, tolerated - or could it be overlooked? - by our painstaking editors. Perhaps this would be the best route of re-entry for the first person into scientific papers; surely it is here that clumsy circumlocutions are most inappropriate. There are two other constructions in which an author may still be able to sneak in a first person pronoun and get away with it: one is the reference to one of a number of joint authors as "one of us" - followed by the initials of the author referred to. The other is in the explanation of italics in a quotation from another author; with the best will in the world most editors boggle at the awful ambiguity of "author's italics".

In view of the editor's privileged use of the first person plural it is most unfitting that authors should be denied the right to use the singular. Editors, please, give us back our eyes.

Brian Hocking

Reprinted with permission from Entomology Division Newsletter, Canada Department of Agriculture 32(6): 1-2, 1954, with minor changes.

## THE SPIDERS (ARANEIDA) OF HAZEN CAMP 81°49'N, 71°18'W\*

R.E. LEECH

Department of Entomology  
University of Alberta, Edmonton

*Quaestiones entomologicae*  
2:153-212, 1966

About 20,600 spiders (Araneida) from Hazen Camp (81°49'N, 71°18'W), Ellesmere Island, Northwest Territories, Canada, were examined. These represent four families and thirteen species: Dictynidae, *Dictyna borealis* Pickard-Cambridge; Lycosidae, *Pardosa glacialis* (Thorell), *Tarentula exasperans* Pickard-Cambridge; Linyphidae, *Collinsia spetsbergensis* (Thorell), *Collinsia thulensis* (Jackson), *Comicularia karpinskii* (Pickard-Cambridge), *Erigone psychrophila* Thorell, *Hilaira vexatrix* (Pickard-Cambridge), *Meioneta nigripes* (Simon), *Minyriolus pampia* Chamberlin, *Savignya barbata* (Koch), *Typhochraestus latithorax* (Strand), and Thomisidae, *Xysticus deichmanni* Soerensen. The known distribution of each species is listed. Detailed descriptions of the rare species and drawings of the structures useful for identification of each species and sex are given. An analysis of the seasonal occurrence of the adults of each species in 1964 and partial results from 1963, showed that all the species were active during the first three weeks following the first day of spring melt, namely June 10 to June 30. Nine species inhabited the humid terrestrial environment, one was present in all environments, and three only in arid environments.

Escape orientation of *Pardosa glacialis* was analyzed in relation to the sun and the observer; reasons for the escape directions are given. The species *Pardosa glacialis* and *Xysticus deichmanni* were found to be parasitized by *Hexameris* sp. (Nematoda, Mermithidae).

The zoogeographical data indicate that there were one or more refugia at or near the northern end of Ellesmere Island during the Wisconsin glaciation and perhaps for the entire Pleistocene epoch. Some of the extant insects and spiders were present in these refugia though most, especially spiders restricted to night shadow areas, have probably immigrated since from more southern localities.

The spiders (Araneida) from the high Nearctic Region are poorly known in every respect - distribution, number of species, natural history, and past history. Previous to this study, the largest single collection of spiders from such a northern location as Hazen Camp (81°49'N, 71°18'W), Ellesmere Island, Northwest Territories, Canada, was the collection made by the Danish Peary Land Expedition of 1947-50, which collected 103 specimens of eight endemic species and one obviously introduced species (Braendegaard 1960). In the winter of 1898-99, the Second Expedition of the "Fram" overwintered at Rice Strait, between Ellesmere Island and Pim Island (78°34'N, 74°45'W) (Bryce 1910), and during the warmer season of 1899, the ship's doctor (my inference) collected some 15 specimens of spiders of seven, possibly eight, species (Strand 1905, and Braendegaard 1936). Collections made by Oliver and others in 1961 and 1962 at Hazen Camp yielded a possible ten species of spiders with only five positive identifications (Oliver 1963).

The purpose of this paper is to give a detailed account of the spiders from Hazen Camp. The account includes data on the taxonomy and natural history, and theories (based on an analysis of the evidence) of the zoogeographic history of the spiders and other Arthropoda at Hazen Camp.

\* An investigation associated with the programme 'Studies on Arctic Insects', Entomology Research Institute, Canada Department of Agriculture (Paper No. 24).



## THE STUDY AREA

The general biology and taxonomy of spiders was studied during the summers of 1963 and 1964 at Hazen Camp, Ellesmere Island, Northwest Territories, Canada (81°49'N, 71°18'W). This is approximately 150 km southwest of Alert, and is on Lake Hazen, the largest fresh water body (78 x 11 km) in the Queen Elizabeth Islands. The study area is on the mid northwest shore of Lake Hazen and extends along the shore for about 5 km and away from the shore for about 3 km. The confines are the Snow Goose River delta, Blister Creek delta, and Mt. McGill. The range of altitudes in the study area is from 158 to 1050 m and includes the following ecological areas: clay plains and slopes, sand, gravel, alkaline clay, *Dryas* hummocks, *Dryas-Kobresia* tundra, marshes, muddy delta, gravel delta, boulder talus slopes, and springy slopes (based on Savile's personal notes of 1962, and Savile 1964, see fig. 1).

Biological work was started at Hazen Camp in 1957 and 1958 (Powell 1961), but entomological studies were not started until 1961 when Donald R. Oliver (Entomology Research Institute, Ottawa) did general collecting and studied pond ecology.

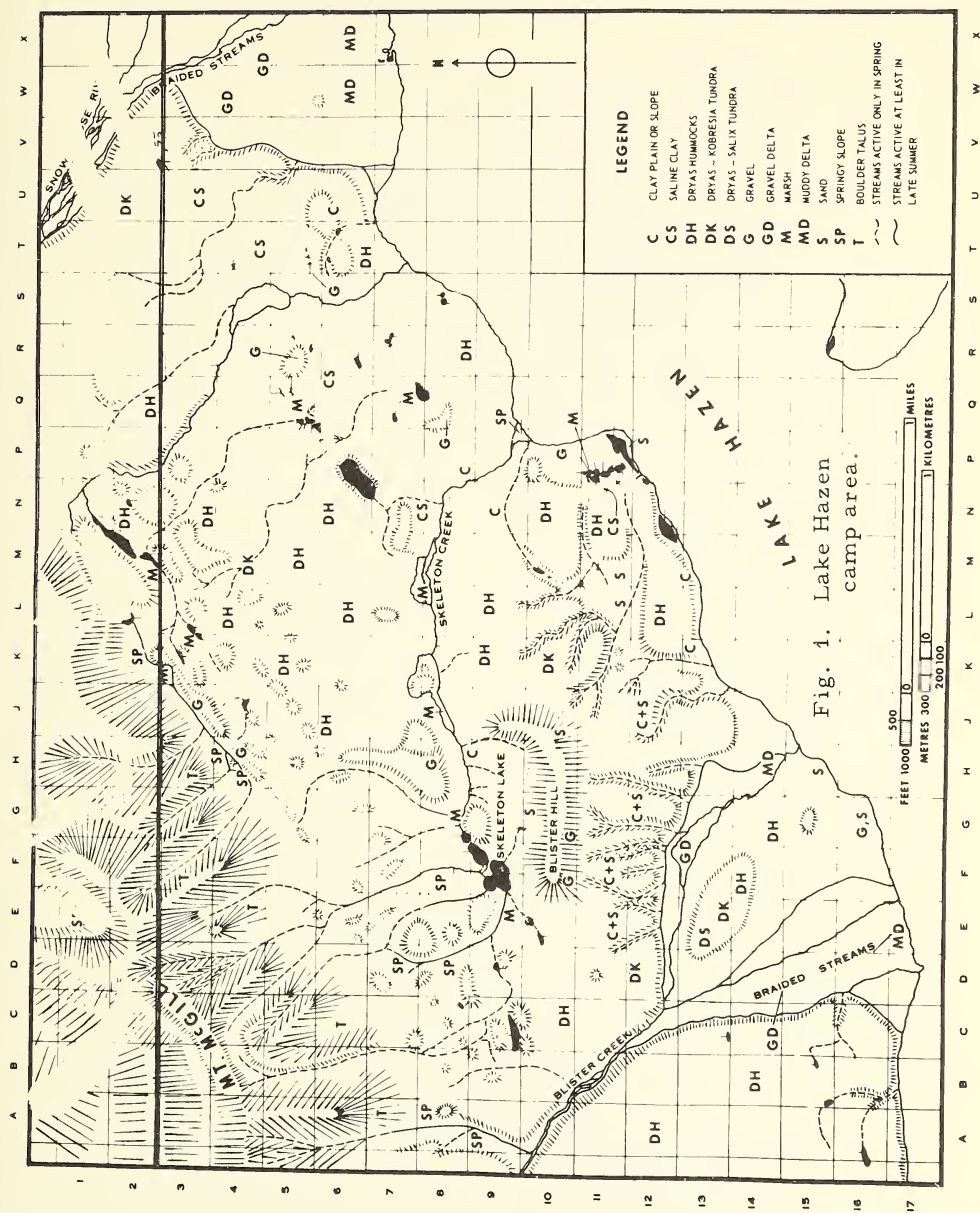
Hazen Camp was opened as an International Geophysical Year station in the late summer of 1957, and since then much information has been published about the Camp and the Lake. Christie (1962) has described the geology; Savile (1964) the ecology and vascular plants; Day (1964) and Yong (1961, *et al.* 1962) have discussed and analyzed the soil characteristics; Oliver (1963) has discussed the Insecta and Arachnida collected to the end of 1962; Jackson (1959, 1960) has analyzed the meteorological conditions; Powell (1961) has discussed the vegetation and microclimate; Harington (1960) reported on snow and ice conditions for the winter of 1957-58; and Hattersley-Smith (1964) published a bibliography of "Operation Hazen", covering the years 1957-63.

**Soil and Soil Conditions**

Soil samples were collected in 1963 from the major habitats as defined by Savile (1964). The depths of permafrost at 12 sites in mid August varied from 40.6 to 99.0 cm with a mean of 73.5 cm. Yong *et al.* (1962) at a comparable period in 1962 reported a mean depth for permafrost of 51.0 cm.

Early in the season, just after the snow has melted, the ground surface becomes a quagmire, but with the sun in view continuously, it becomes firm in two to three weeks except in marsh or pond depressions. The period when the snow and ice leaves the surface of the ground will be referred to as "spring melt".

Very little of the surface soil is without frost-heave cracks. The cracks vary from 0.1 to 5 cm wide, from 1.5 to 40 cm deep, and from 10 cm to several metres long. Organic content of the soils varied from 0.3 to 19.6% with a mean of 4.1%. The pH was usually between 7.4 and 8.6. Soil temperature maxima at the surface were generally 7.5 to 16.5°C higher than air temperature maxima on sunny days, and minima were 2.5 to 5.5°C warmer than air minima on overcast days (Powell 1961). On June 6, 1964, one day before the spring melt, I recorded the following



temperatures in bright afternoon sun on a 20° south-facing slope: 2.5 cm above soil surface.... 2.7°C, at surface.... 6.3°C, 2.5 cm below soil surface.... 9.9°C.

In appearance, the soil is mostly sandy to sandy-clayey with moderate to sparse vegetation cover.

### Vegetation

There are about 115 species of vascular plants recorded from the Lake Hazen region, but there are only a few abundant ones. These are *Salix arctica* Pall., *Dryas integrifolia* M. Vahl., *Kobresia myosuroides* (Vill.) Fiori and Paol., *Carex aquatilis* Wahlenb. var. *stans* (Drej) Boott., *Cassiope tetragona* (L.) D. Don., and in restricted areas, *Eriophorum Scheuchzeri* Hoppe, and *E. triste* (Th. Fries) Hadac and Löve. The remaining plant species are sparsely distributed throughout the study area.

### Climate and Weather

Detailed records of the weather have been made for the years 1958, 1961, 1962, 1963, and 1964. The lowest winter temperature recorded by the minimum thermometer at Hazen Camp is -70.6°F (-57.0°C) during the winter of 1963-64 (personal record). Figure 2 is a graph of the cumulative day-means of Stevenson screen temperatures to date since June 1 at Hazen Camp, 100 metres from the lake shore, 1.8 m above the ground, and 161 m above sea level.

For the latitude, the summer temperatures are exceptionally high, often higher for long periods than at many nearby coastal stations. The inland position of Lake Hazen accounts for the higher temperatures. The lake is in a very stable high pressure trough region, and is in the shadow of the Garfield Range to the north and northwest.

Precipitation at Lake Hazen is very light. Jackson (1959, p. 95) recorded 0.98 inches (2.48 cm) water equivalent during the period August 1957 to August 1958, and the station at Alert recorded 4.52 inches (12.8 cm) during the same period. Snowfall between September and May accounted for 91% of the precipitation at Lake Hazen.

Despite the low precipitation at Lake Hazen, considerable moisture is available for the plants and animals. During most summers (1964 was an exception) the melting of snow and ice from the surface is sufficiently slow that the ground surface is dry for only two weeks before the water from permafrost melting comes to the surface. As the permafrost water percolates to the surface, depressions that were full of water during the spring melt and which had dried up during the course of the summer, refill.

The wind speed averages at Lake Hazen are very low with over 76% of the yearly observations being 5 mph or less, 16% from 6-10 mph, and 8% 11 mph or over. The majority of the winds come from the northeast, along the Lake Hazen trough (Jackson 1959, p. 125).

Relative humidities in 1962 and 1963 were read every 6 hours at 1.6 m above the ground, and give daily mean figures of 80-88% for June, and 76-80% for July and early August (Savile 1964, p. 240), but were much lower during the summer of 1964 because of continuous high winds from the southwest. The prevailing low-speed winds permitted conditions

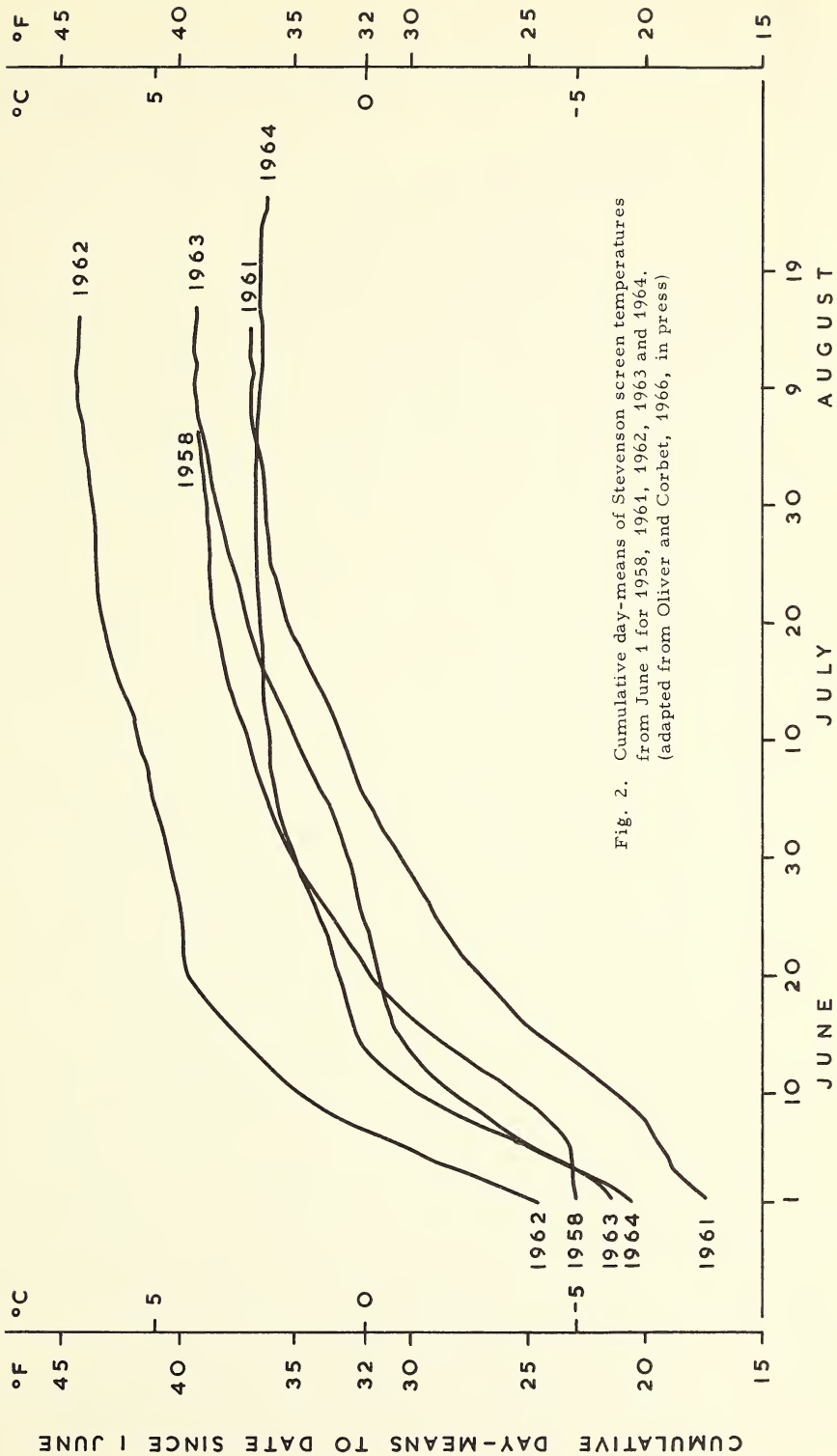


Fig. 2. Cumulative day-means of Stevenson screen temperatures from June 1 for 1958, 1961, 1962, 1963 and 1964. (adapted from Oliver and Corbet, 1966, in press)



of almost 100% relative humidity to exist at or near the surface where the shearing effect of the ground on the wind caused little disturbance of the air at one foot (30 cm) or less (composite data, Jackson 1959 , pp. 127-130, and my notes).

During the summer Lake Hazen enjoys cloudless periods for two to three weeks without interruption.

#### **Night Shadow Areas**

In 1963 and 1964 I observed that several species of the spiders were restricted to the night shadow areas. These areas are in the mountain shadow for a minimum of about four to six hours during each 24 hour period at the warmest part of the season, and longer earlier and later in the season. The shadow period is synchronous with night-time in more temperate regions at this longitude. The shadow area extends from the shoulders of Mt. McGill to the linemarked off as map coordinates K3 to K6, J7 to J9 to B9 and all the area encompassed (see fig. 1).

### **MATERIALS AND METHODS**

Previous to 1963, possibly ten species of spiders were known from the Hazen Camp area from fewer than two hundred specimens. The program "Studies on Arctic Insects" was instigated by D.R. Oliver of the Entomology Research Institute, Ottawa, and has dealt so far with insects from Isachsen, Ellef Ringnes Island, (McAlpine 1965), and Hazen Camp, Ellesmere Island, (Downes 1964; Oliver 1963). I was given permission to study the spiders from the Hazen Camp area. Studies were begun at the end of June, 1963, and continued until the end of August, 1964, with an interruption during the winter of 1963-1964.

#### **Materials**

The structure, identification, and distribution of 20,534 spiders comprising 13 species collected during two summers within the study area were examined. All were collected in the Hazen Camp area. Identified also were 751 spiders from Melville Island (collected by Larry Law), 36 spiders from Tanquary Fjord, Ellesmere Island (collected by Guy Brassard), 18 spiders from Bathurst and Cornwallis Islands (collected by Leonard Hills), and 54 spiders from Thule, Greenland (collected by me). About 522 individuals of two species of Lycosidae were studied in an attempt to determine the length of life cycle.

The field equipment included 50 aluminum cake pans, 23 x 23 x 6.5 cm, used in 1963 and 37 pans used again in 1964. Each pan contained the following fluid mixture to a depth of 2 cm: 600 ml water, 400 ml ethylene glycol, 5 ml formalin, and 1-2 ml of any liquid detergent.

Identifications in the field laboratory were made with the aid of a Wild M5 binocular dissecting microscope with a maximum power of 50 diameters. Identifications, drawings, and analyses in the laboratory were made with a Leitz binocular dissecting microscope with a maximum power of 150 diameters and a 100 watt zircon arc lamp ("Mikrark Illuminator", made by the Boone Instrument Corporation of New York). A

Leitz eyepiece grid 10 mm square divided into 0.5 mm squares and a 10 mm eyepiece micrometre scale with 100 divisions were used in conjunction with millimetre graph paper in preparing the drawings.

The meteorological equipment of Hazen Camp was set up and used throughout the study periods. Equipment included corrected maximum and minimum thermometers, a Feuss corrected millibar barometer, a hygrothermograph, and an anemometer.

A pair of each species will be sent to the following institutions or persons: American Museum of Natural History, New York; Zoologisk Museum, Kystalgade, Copenhagen; Zoological Institute, Uppsala University, Uppsala; Laboratoire de Zoologie, University of Toulouse, Toulouse; Dr. Hermann Wiehle, Dessau; Museum of Comparative Zoology, Harvard University; Department of Entomology, University of Alberta, Edmonton. The remaining specimens will be deposited in the Canadian National Collection, Ottawa. Ten males and 10 females of *Tarentula exasperans* Pickard-Cambridge, 1877, will be sent to the Zoologisk Museum, Copenhagen.

#### Methods

The study area was examined for the principal ecological zones (based on Savile's notes of 1962). In 1963, a total of 50 traps was placed at carefully selected sites and in 1964, 37 traps were used. Eight of the sites in the habitat of some of the less-frequently collected species were used in both years. The new traps of 1964 were in areas not examined in 1963.

The traps were examined once every four days. This interval was selected in 1963 in order to fit into a previously established work pattern, and retained in 1964 for purposes of continuity. Each trap was emptied of spiders and insects and the fluid was replaced or added to.

The traps were set so that the lip of the pan was flush with the ground level. There was usually very little sand drift except in some sites because wind speeds were low. Traps placed in low regions near streams were often flooded by water and the specimens lost. The biggest problem was caused by foxes and wolves which would urinate and defecate into the traps, then scratch sand and any loose vegetation into them. I have interpreted this to mean that they dislike either the pans or their contents. Oliver (pers. comm.) and B. Hocking (pers. comm.), after observing similar behaviour in these animals, have interpreted these actions in the same way. There did not seem to be any way to solve this problem!

Spiders from each trap were preserved and kept in separate vials by trap and by day. Individual spiders were identified to species in the field laboratory. The results of examination of this material are recorded by species on graphs in the text. Identifications were checked, and numbers of individuals per sex per day per trap were also recorded at this time. My analysis of a species habitat is based on where the immatures and females of a species were collected, as males wander. Overwintering sites were used as further evidence of the usual habitat of a species. Except for four species, the immature stages were not identified as identification of immature stages can never be positive. Individuals

with anomalies in epigyna and pedipalp organs were examined for mermithid (Nematoda) or other parasites.

All measurements and drawings were made from the microscope. The pertinent sexual parts of large spiders were drawn at 54 diameters, and for the smaller species, at 150 diameters. Measurements of all parts were recorded with each drawing.

Measurements of carapaces were made from directly above the spider. Length is the distance from the base line between the posterior median eyes posteriorly along the midline to the incurve of the hind edge of the carapace. Carapace width was measured at its widest part. The opisthosoma was measured from the dorsal aspect. Total length of the spider was measured from the dorsal aspect from the base line between the anterior median eyes to the end of the opisthosoma.

Measurements of legs and leg parts were always made on the actual dorsal side of the leg. Measurements were made from the proximal to the distal part of a leg segment and did not include the membranes at the joints. Trichobothrium is abbreviated in the text as Tm. The position of a trichobothrium on the metatarsus is expressed as the ratio of its distance from the proximal joint to the total length of the metatarsus. This is expressed as a decimal fraction.

#### Dictynidae

*Dictyna borealis* Pickard-Cambridge, 1877 p. 273 (Figs. 38, 39)

*D. borealis*: Bonnet 1956 p. 1431; Holm 1958b p. 534; Braendegaard 1960 p. 7; Chamberlin and Gertsch 1958 p. 136 (in part). *Dictyna* sp. Oliver 1963 p. 176.

*Notes on taxonomy* - Chamberlin and Gertsch (1958, p. 137) place a few specimens collected by H.W. Levi in the high mountains of Colorado in this species, but the tips of the emboli of those specimens differ in shape from the emboli of specimens collected at Lake Hazen. The latter are definitely members of the species *borealis*. Further, the Colorado specimens are considerably larger than any of the Lake Hazen specimens. Gertsch (pers. comm., 1965) has confirmed my opinion that the Colorado specimens are not *borealis* Pickard-Cambridge, even though they are similar and probably related to the species.

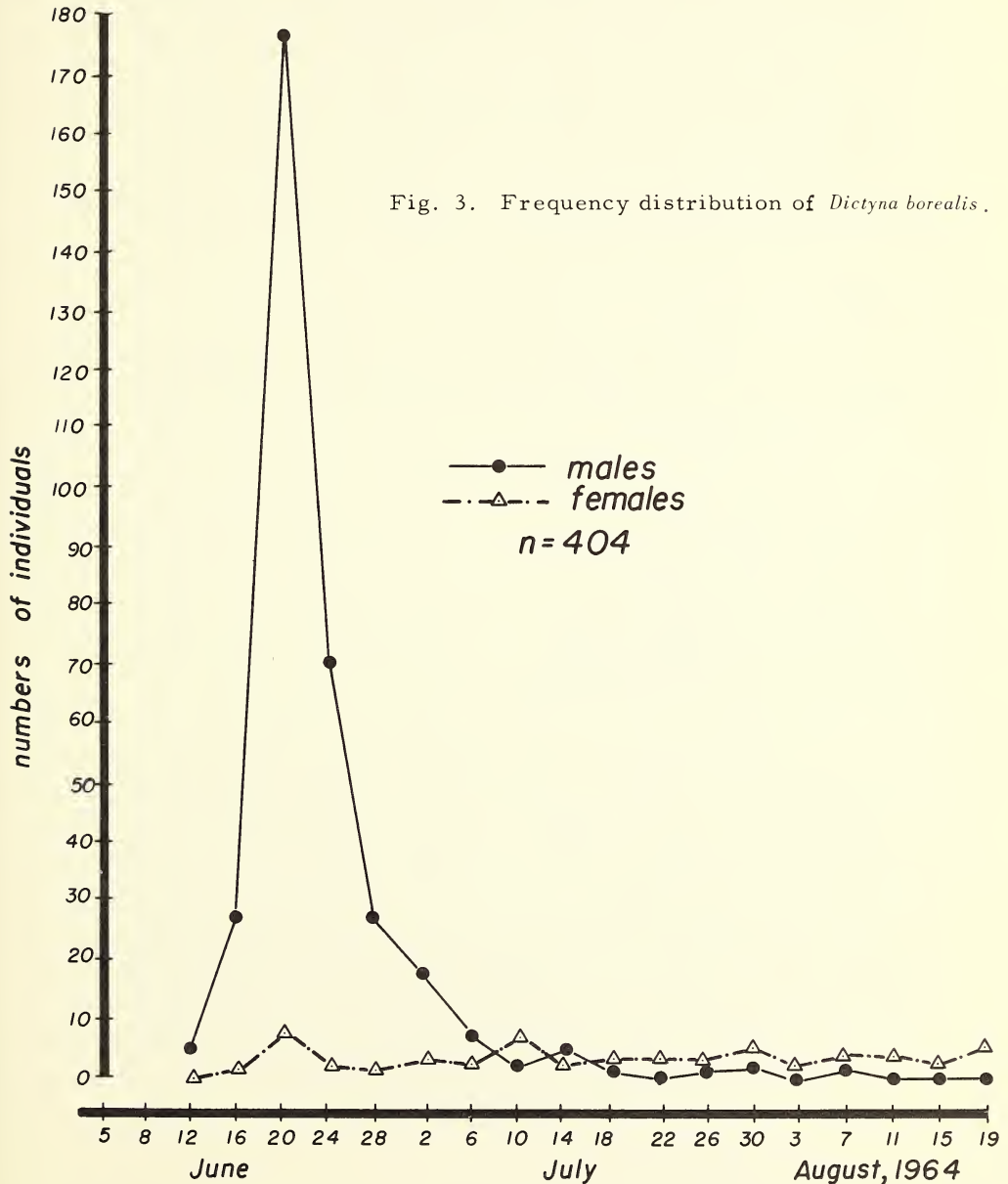
*Natural history* - This species is a member of the arid arctic faunal element (Braendegaard 1946) and is heliophilic. Specimens are most frequently found on dry, south-facing slopes exposed to the sun, with a vegetation consisting mainly of *Dryas integrifolia*, but often of *Cassiope tetragona*. It prefers hummocked, almost wind-free areas. It overwinters in the vegetation on the surface.

Figure 3 shows the main period of activity of the males of this species. The females are rarely wanderers. The main activity of the males is directly correlated with the courtship and mating periods of the species. The adults are not known to overwinter.

Courtship was not observed in this species, but it cannot be long nor involved, as virgin males and females introduced to one another were found mating within a 45 min lapse of observation. Previous to mating, the males assumed small territories which they defended against all

other males, but which females seemed almost coaxed to enter. Defending a territory consisted of actively fighting all male intruders.

Four pairs of spiders were observed mating and both of the male pedipalpi were inserted into the female at the same time. The male was positioned ventral to the female, with the carapace of the male almost touching the prosomatic sternum of the female. There did not seem to be any specified angle as two pairs were lying on their side, the third pair positioned with the female upside down, and the fourth pair with the female rightside up. Mating continued for about 30 min, then each of the four pairs began separating. They did not recouple. Males did not mate more than once.





In 1963, I observed that females of *Dictyna borealis* almost invariably deposited their egg sacs and built their webs on the south- and southwest-facing sides of *Dryas integrifolia* hummocks and in the vegetation, but never on the ground. About 30 egg sacs were seen. Laboratory specimens in 1964 also laid eggs in the vegetation. Females remained near the eggs until they hatched. Ten egg sacs were examined and found to contain from eight to thirteen eggs, with a mean of 8.7 eggs per sac.

This species appears to be able to overwinter at any stage except the adult.

When offered a choice of over 30 species of Diptera, this species preferred small ones. Chironomidae and Ceratopogonidae were the main preferences. Cyclorrhaphous Diptera were always refused. No parasites or predators of this species were found.

*Material examined* - About 625 adults of this species were examined, and all were from Hazen Camp area.

*Distribution* - Greenland (Peary Land; E. Greenland, 68-77°; W. Greenland, 60-79°N). Ellesmere Island (Hazen Camp area). Bernard Harbour, (58°48'N, 114°W), Mackenzie District, N.W.T.

This species appears to have a relict distribution (fig. 4), though as it is able to balloon, it should be found in more of the Nearctic Region.

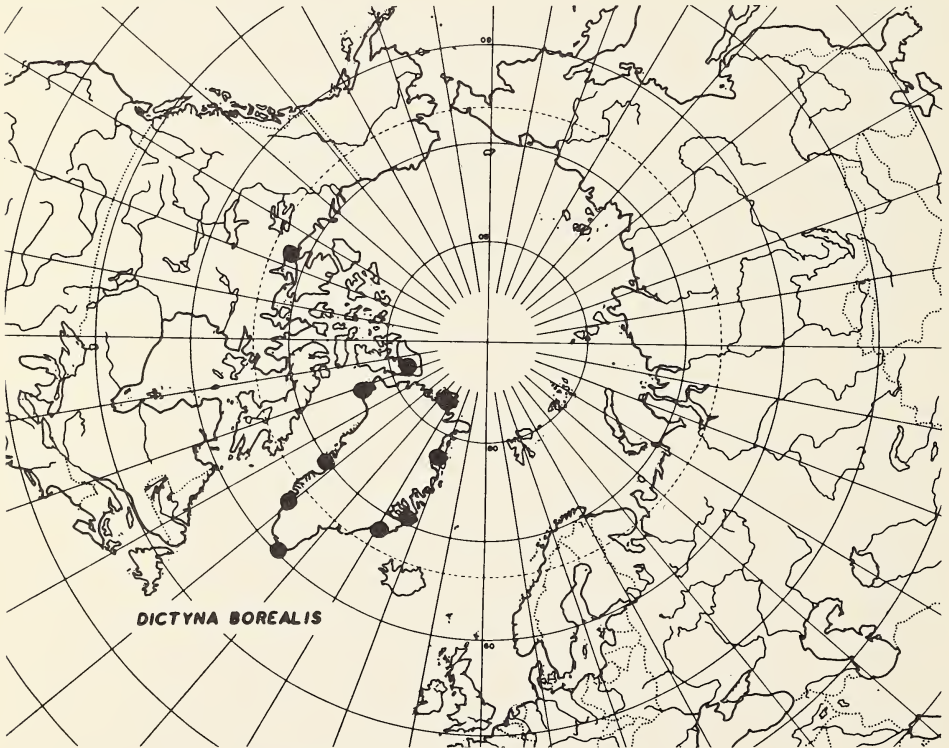


Fig. 4. Distribution map of *Dictyna borealis*.

**Lycosidae**

*Pardosa glacialis* (Thorell) 1872b, p. 159 (Figs. 32-34)

*Lycosa glacialis* Thorell 1872b, p. 159. *P. glacialis*: Bonnet 1958 p. 3371; Oliver 1963 p. 176. *L. glacialis*: Holm 1958b, p. 529; Braendegaard 1960 p. 8.

*Notes on taxonomy* - This species is a member of the genus *Pardosa*, and not of the genus *Lycosa*. The characters of both genera are summarized in Kaston (1948, pp. 321, 331). The egg sacs of *Pardosa glacialis* are a pale green-blue and are lenticular. Those of all known *Lycosa* are white and spherical.

*Natural history - Habitat* - This species belongs to the euryoeuous (euryecious) arctic faunal element (Braendegaard 1946). Specimens are found everywhere except in windy places. *P. glacialis* overwinters in the soil in cracks and under stones on the surface. It has not been found in the overwintering sites at depths greater than 2.5 cm. It does not burrow. Individuals of this species drown easily, hence they will not be found overwintering alive in areas that are inundated or soaked by spring melting of snow and ice. Apparent migrations or mass movements of individuals in the spring are really the successful overwintering individuals radiating from winter quarters.

Figure 5 shows the main period of activity of the males of this species to be between June 29 and July 6. The activity period of males is directly correlated with the courtship and mating period of the species. The adults are not known to overwinter.

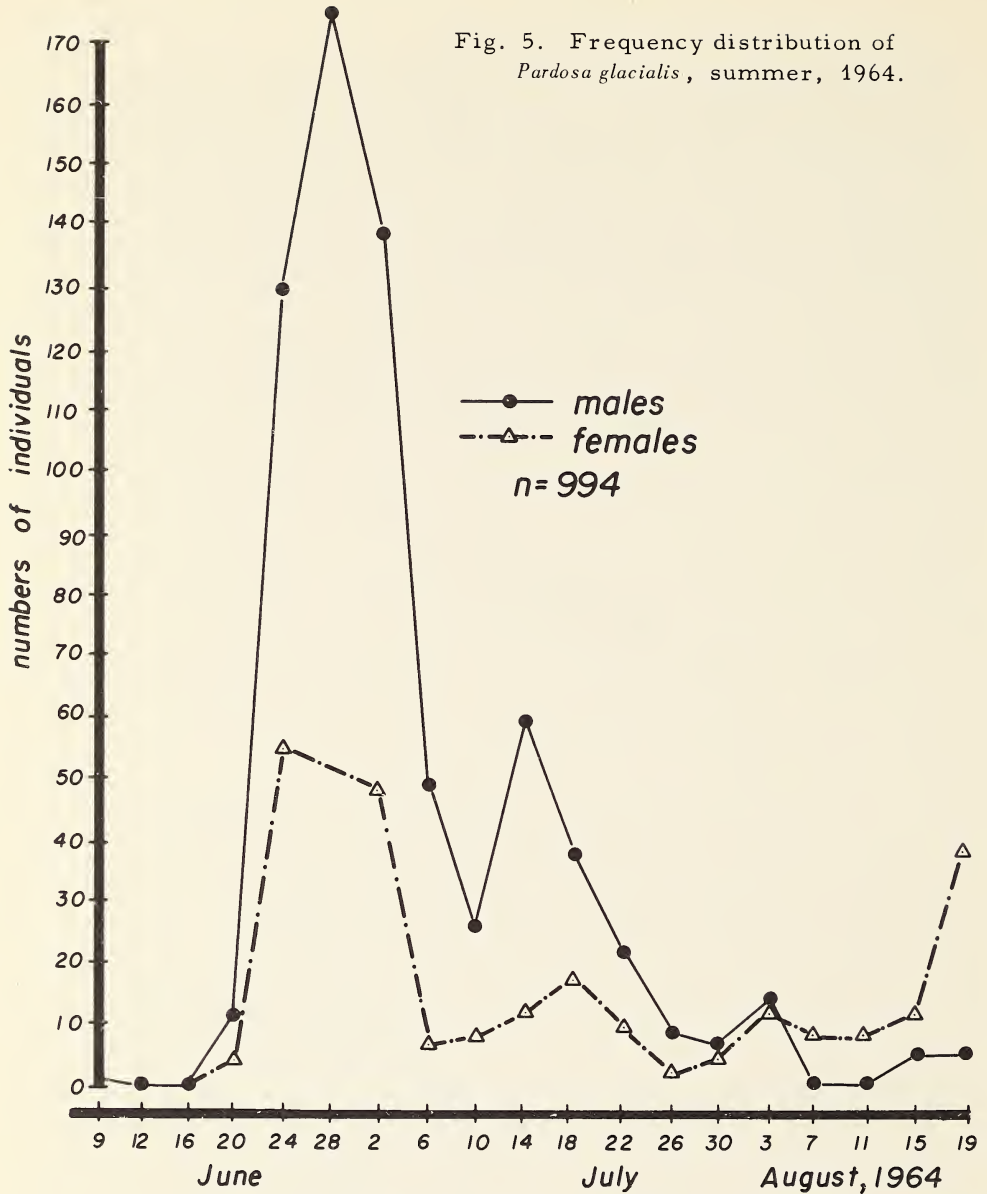
*Natural history - Courtship* - The courtship and courtship preliminaries were observed from the beginning of the season. On June 29, 1964, the eighth day after moulting from the penultimate instar, captured adult males and females suddenly became active in courting. It was noted that the males would court under natural conditions only if heat and light were sufficient. In the laboratory, it was noted that courting started or stopped if a 100 watt bulb were brought to 25 cms or taken away to 75 cms.

When courting was first observed, the males began holding a small territory, and would defend this against all intruders except females. In all, 63 males were observed courting females, 46 in the laboratory and 17 under natural conditions. No variation in courtship was observed.

The males were often seen rubbing the substrate with the venter of the opisthosoma, but sperm webs were never seen. Evidently some species of lycosids spin sperm webs (Gertsch 1949, p. 73) and some do not (Savory 1928, p. 224).

Courtship is summarized as follows: on June 29, 1964, a male was observed in the beginnings of courtship. The palpi, bent downward at the patellae, were moved in a circular motion which, when viewed from above, appeared clockwise in the right palpus, and anticlockwise in the left. Simultaneously, the first pair of legs were lifted and extended horizontally forward, then gradually relaxed while extended. When the tarsi of the first legs touched the ground, the palpi stopped churning. The palpi started rechurning when the legs, brought back toward the carapace and raised, started extending forward.

Fig. 5. Frequency distribution of  
*Pardosa glacialis*, summer, 1964.



Associated with these waving motions was a characteristic weaving of the body. First, the waving motions were started in a position which squarely faced the female, who was usually some 10 cm distant. The male then turned  $30^\circ$  to the left and vigorously made the waving motions, turned toward the female and repeated the waving, then turned  $30^\circ$  to the right and again repeated the waving motions, then centre, then left . . . until within two cm of the female, at which point the weaving was cut to two positions, each about  $20^\circ$  from centre. The right-left weave and associated waving motions were continued vigorously until either the female chased the male away, or until their legs touched, at which point the female suddenly assumed a defensive position with fangs spread open

and the first two pairs of legs raised up and forward. In this position, the female charged forward for about one cm, and the male fled for about 15 cm, then turned and again started the same advance procedures. Almost invariably, the males approached the females from the front.

On June 30, 1964, most of the males were dead. Mating had presumably taken place in the late afternoon of the previous day.

Previous authors have argued whether the male's courtship reaction was precipitated by sight, smell, contact, or a combination of all three. It is my opinion that courtship by individuals of *P. glacialis* was initiated by chemo and contact stimuli rather than by sight or touching of the ground over which the females had passed. The opinion is based on the following observations. Virgin males placed in cages that had previously held females did not become "excited", but virgin males placed in cages with females present became "excited" by leg contact with the females and began courting within 25 minutes. The initial reaction of the males after contact was to withdraw to a corner and start cleaning the whole body, legs, and palpi. The cleaning usually lasted about 20 minutes. The males then ventured out slowly, and at first fled at the approach of either a male or a female. Courting began shortly thereafter. Osterloh (1922) rightly concluded that the necessary stimulus for male spiders is different in different species. The condition of the male and female should be known when the observation was made. For instance, had observations at Hazen Camp been made only on males that had previously touched females, the conclusions might have been that sight is the "triggering" mechanism.

Mating was never observed in *P. glacialis*, but one male which had repeatedly been shunned by all females, began courting a large male Chironomid, which was lying on its side almost dead. The male eventually mounted the fly in the usual *Pardosa* manner (Kaston 1936, p. 167), it then discovered the mistake and ate the fly.

*Natural history - Egg laying* - Within 48 hours after mating, the females were ready to lay eggs. Four females were observed during the whole egg-laying process. Because there were no observable differences during the egg-laying, the general pattern is described as follows. The female located a sheltered flat place which lay pocket-like between and under several rocks. She then started making a thin flat sheet of webbing about 2.5 cms in diameter. In the centre of this the female made a small, much-thicker patch of webbing about 0.8 cm in diameter which was of a different silk material than the main sheet web. The centre patch was slightly green and opaque. These preparations took about 30 min.

The female then placed her genital region over the small centre patch and started laying eggs at the rate of one egg each 50-60 seconds until the usual 50-53 eggs were laid. Each female appeared to rest for about ten minutes, then made the covering for the sac. The silk material for the upper and lower halves of the egg sac was the same. The upper half of the sac was attached to the lower half with such firmness that the lower half became somewhat bowl-shaped when only half the upper covering was made.

The female made the cover for the upper half by attaching a thick



silk line to one side of the centre patch, then swung the opisthosoma up and over the eggs to the far side. As the silk lines were attached, the female rotated about the eggs making a complete cover. This operation lasted about 35 minutes. Again the female rested before cutting the egg sac free with either the chelicerae or endites. The female then turned and placed the spinnerets over the sac and attached them to it. The female then waited for over an hour, emerged from the hole with the sac attached, and the opisthosoma tilted up so that the sac did not drag on the ground.

I was not able to keep any of the caged females alive until the young emerged. Whenever a female died, I examined the egg sac to note the development of the eggs, but in no case were any young seen. On August 19, 1964, a female was captured with young that had just hatched from the egg sac. These were the only young seen of this species that hatched in 1964.

*Number of instars and longevity* - On the basis of analysis of mensural data obtained from 318 individuals of this species, it appears that there are seven instars from the egg to the adult (fig. 6). The first instar is spent inside the egg sac, and the second instar emerges from the egg sac and crawls onto the opisthosoma of the mother. If it is assumed that on the average each instar lasts one year, then the length of the life cycle of this species is about six years.

*Solar escape orientation* - Three groups of specimens were used for the experiment, one group encountered in the field and left alone except for the period of encounter, and two groups that were captured. One of the captured groups was kept outside where the sun could be seen on clear days. This group was maintained in order to assure having a control group to contrast with the group kept in the laboratory. The second captured group was maintained in the laboratory with a 100 watt bulb shining from the geographic east about 25 cm from the cage. The purpose of maintaining this group was to see if the solar orientation could be interrupted or disturbed, and that this occurred is apparent from the results summarized in figures 7, 8 and 9. The longer the specimens were kept in the laboratory, the greater became their confusion when released. Directions were often so unsure that a spider would turn almost  $360^\circ$  in a 5 cm circle before slowly going in a direction, and then it was as often towards as away from the sun rather than at right angles to it, as seen from the charts of the specimens kept outside or encountered in the field (figs. 7, 8, & 9). Each specimen used in the laboratory experiment was kept inside for a minimum of nine days before being used in the experiment. In no case was the same spider tested more than once in a three hour period, as it was found that individuals became tired and gave different initial results at each escape.

Experiments were begun on July 2, 1964. Only adults or subadults were used as the younger spiders showed preference for well-protected, vegetated areas and their escape reactions were either to remain still or else hide in the vegetation. Parasitized adults and subadults were also omitted from the experiment when it was found that their escape reactions

were considerably altered. The parasitized spiders show little or no escape reaction. In fact some refused to move unless prodded with a stick.

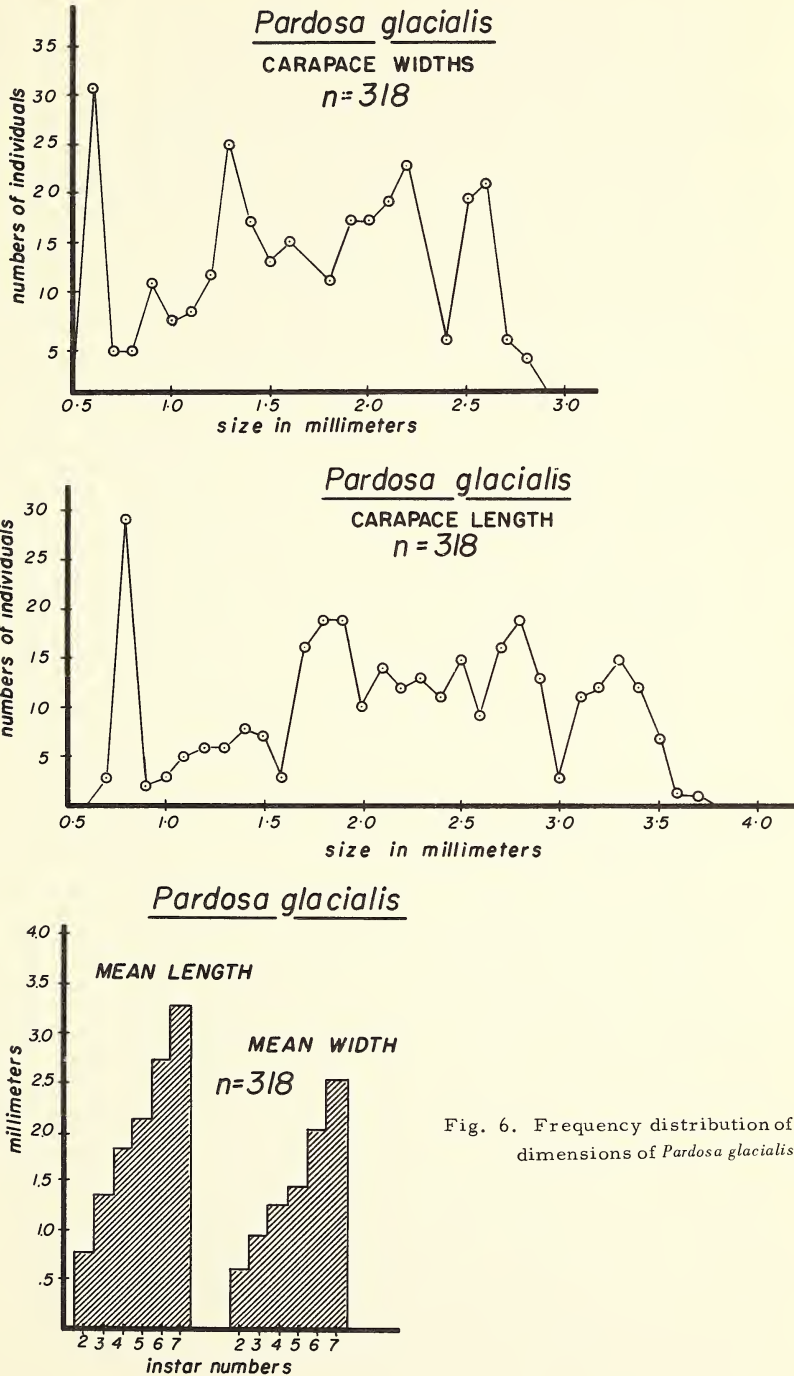


Fig. 6. Frequency distribution of dimensions of *Pardosa glacialis*.

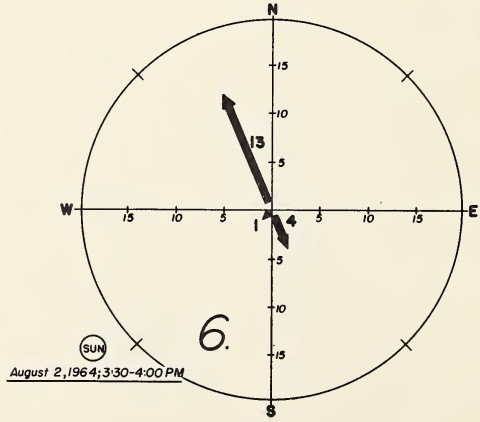
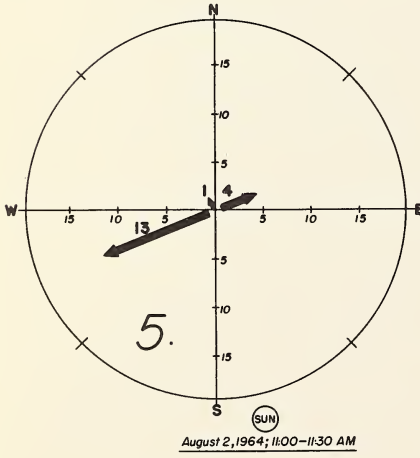
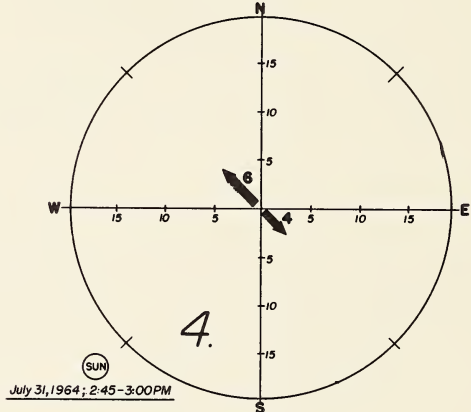
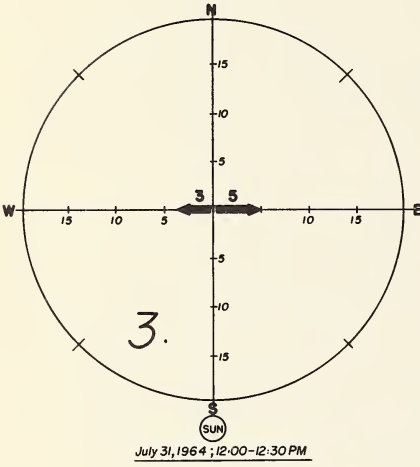
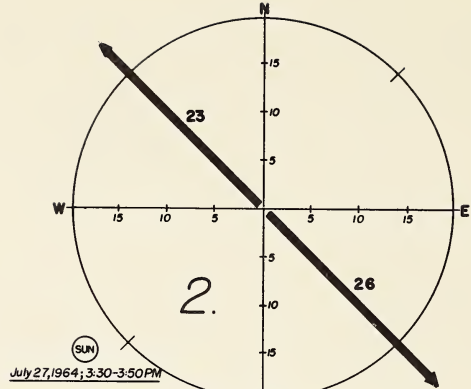
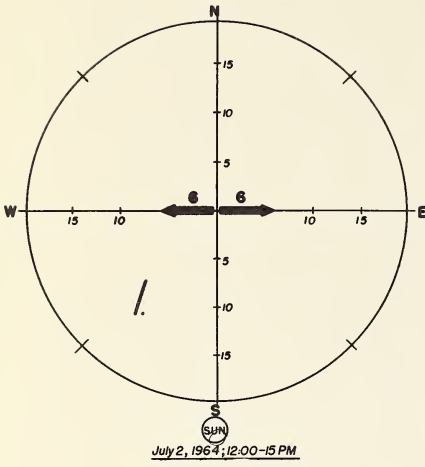


Fig. 7. Escape directions of *Pardosa glacialis* in the field observed under natural conditions.

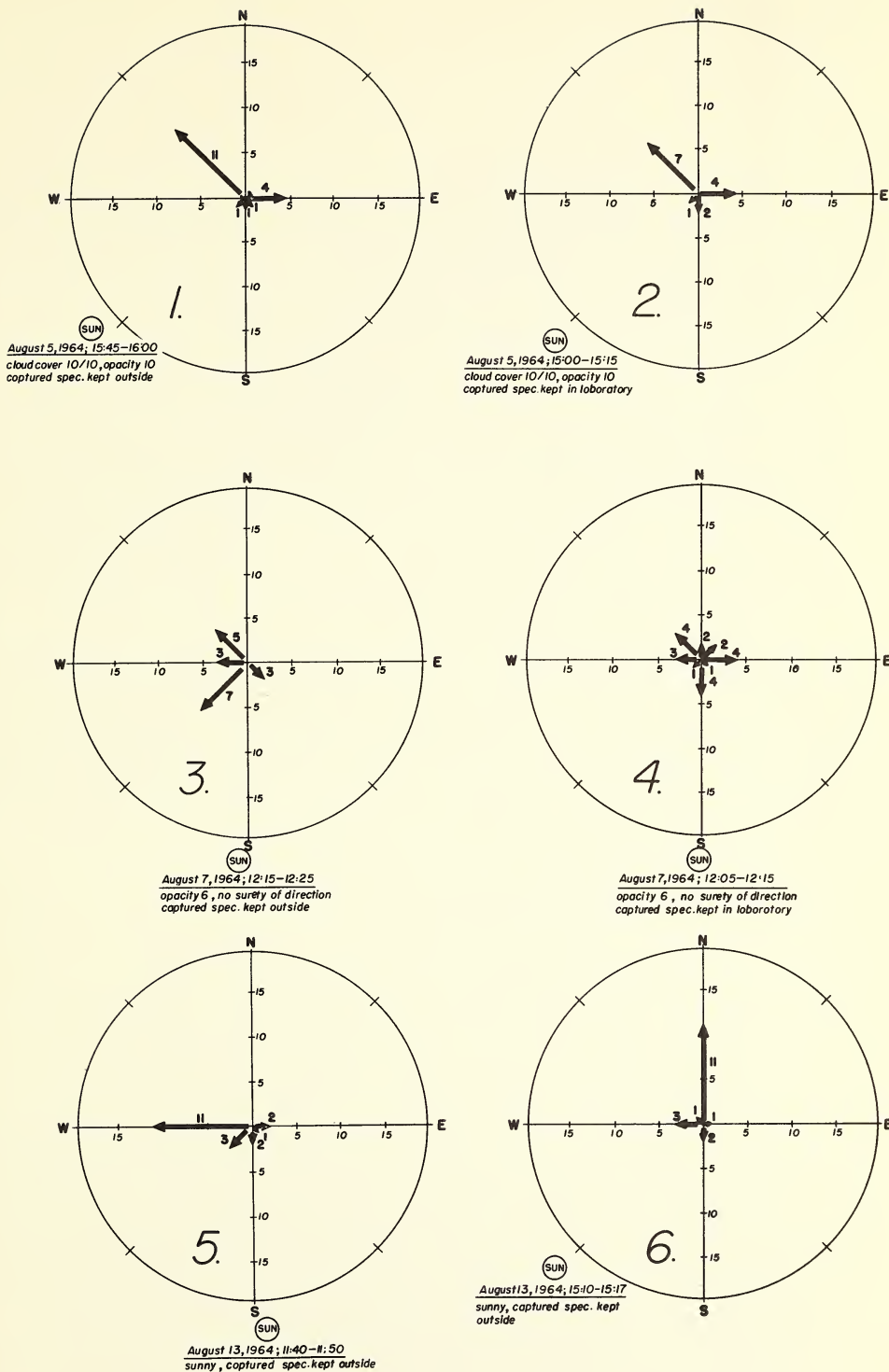


Fig. 8. Escape directions of specimens of *Pardosa glacialis* kept in sunlight and specimens exposed to a 100 watt lamp shining from the east.



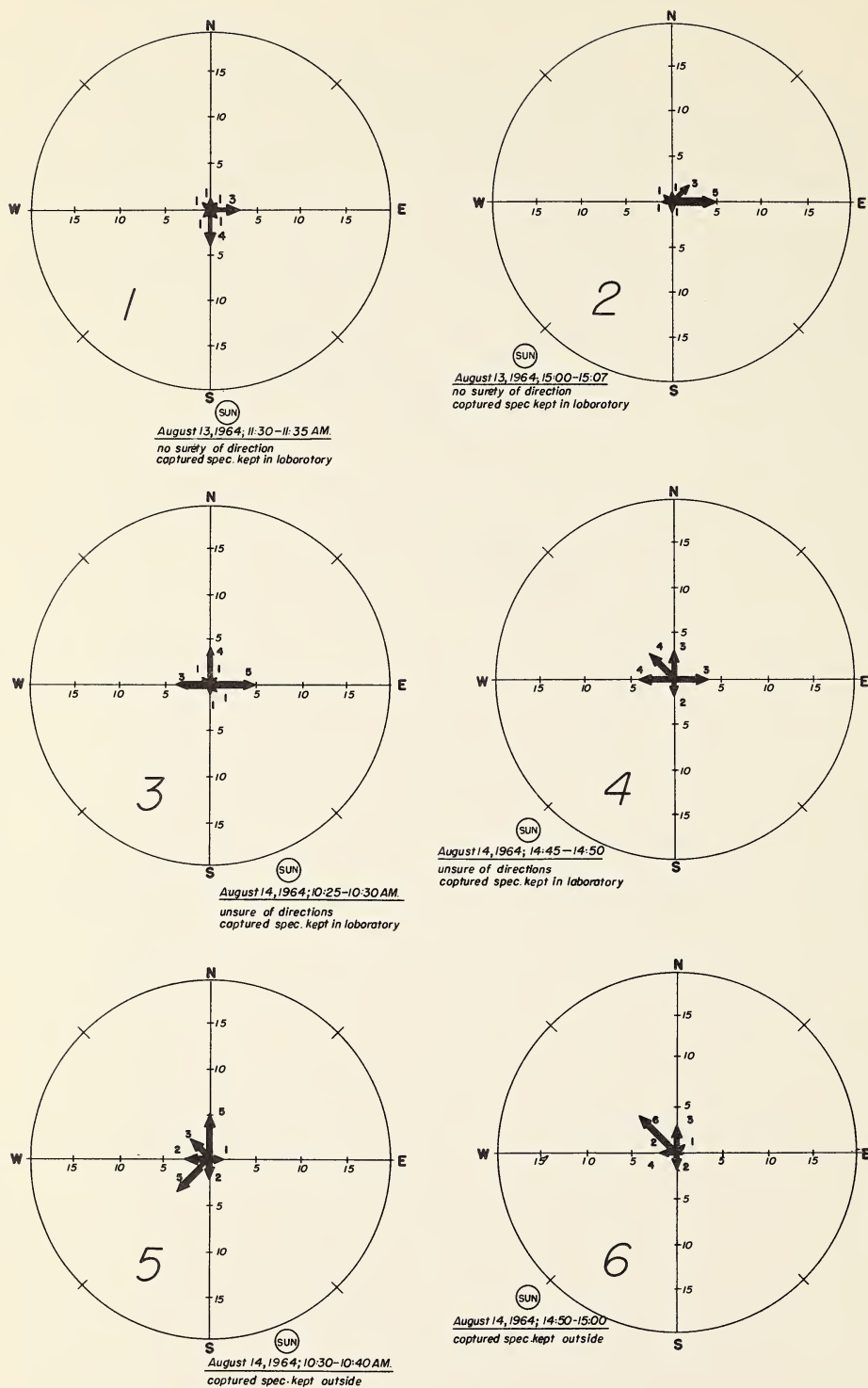


Fig. 9. Escape directions of specimens of *Pardosa glacialis* kept in sunlight and specimens exposed to a 100 watt lamp shining from the east.

The results of the Lake Hazen experiments are as follows: *Pardosa glacialis* encountered in the field or kept under somewhat natural conditions attempted to escape at approximately 90° right or left to the sun's position. The group kept in the laboratory showed, in time, almost complete disorientation of escape direction. Individuals encountered in the field and placed in the shade before being startled, escaped directly away from me, but upon entering the sunlight, turned and ran at 90° to it. Aged or senile individuals tended to show less and less orientation as the season progressed. Cool weather also inhibited escape reactions as spiders apparently tried to get warm rather than escape.

I suggest that the escape direction of *Pardosa glacialis* in relation to the sun - that is, to the right or left - is not intrinsic to each individual, but a function of the direction in which the spider is facing, at rest, immediately prior to the time of the escape. The spider's resting position is one that will allow it to present most of its body to the sun at one time. In mid-afternoon, for example, this would mean on a line running northwest to southeast, and from the graphs it can be seen that most of the spiders tried to escape to the northwest (figs. 7.2, 4, 6; 8.1) or southeast (fig. 7.2, 4, 6).

Papi and Syrjämäki (1963) have conducted similar experiments with *Arctosa cinerea* (Fabr.) (Lycosidae), but have obtained different results. They have combined results of testing periods of rather long duration -- usually six hours. I feel that for these experiments long periods obscure the results. Therefore, I have recorded results for 15-25 minute periods so that variations in the spiders' reactions can be more easily observed in relation to variation in the sun's position. Tests were made in the mid-morning and again in the late afternoon. Further, no theoretical escape direction has been assumed or considered.

*Food, parasites & predators* - This species fed most readily on Chironomidae, and when hungry, fed on the smaller cyclorrhaphous flies. Blow flies and other flies of this size were left untouched. The species is also highly cannibalistic, but was not observed feeding on other species of spiders.

Remains of *P. glacialis* were found in the crops and gizzards of several snow buntings and knots. No previous information about vertebrate predators of this species was found.

Various degrees of parasitic castration in male and female *P. glacialis* by nematodes of the genus *Hexameris* (Mermithidae) have been observed at Hazen Camp. About one per cent of the specimens collected were infected and most of these were females. Possibly more careful examination of all the Hazen Camp specimens of *P. glacialis* might reveal a considerably higher rate of parasitism, for a parasitic infection is very hard to detect in the young spiders.

The ultimate effect of the parasite on the spider is death, as just before *Hexameris* emerges from the opisthosoma of the spider, the essential organs of the spider are eaten. Spiders examined just after a parasite had emerged were found to be lacking in the main prosomatic muscles, the entire digestive system, fat body, and the entire reproductive system. An infected spider usually stopped feeding about one week before the

parasite emerged, and during the last week such spiders were seen drinking quantities of water.

When the parasite was about to emerge, the spider crawled into a dark hole or corner. It took about 20 minutes for *Hexameris* to emerge completely from the anterior end of the opisthosoma. The spider died 30-60 minutes before the *Hexameris* first emerged.

Some of the obvious external morphological characteristics for *Hexameris* infection are these: lopsided or greatly enlarged opisthosoma; epigynum altered from the normal; legs shorter and thicker; sluggish or inactive spider; and some secondary sexual characteristics of the male not present or barely developed. A normal male appears gaunt and thin, but a parasitized male appears fat like a female full of eggs.

Parasitic castration in lycosids by *Mermis* has also been described by Åke Holm (1941) and some examples that might be caused by parasites are cited and illustrated by Kaston (1961, 1963a, 1963b).

*Material examined* - Approximately 3383 adults of this species were examined from Hazen Camp, one female from Payne River (59°30'N), Quebec, four males from "Manitoba", one male from Umiat, Alaska, four females and three males from Mesters Vig, E. Greenland, six females from Holsteinborg (approx. 63°N), W. Greenland, and one female from Axel-Heiberg Island (Heinz Rutz, collector, 1963).

*Distribution* (fig. 10) - Greenland (East, 68-77°N; West, 61-75°N; Peary Land, 82-83°N). Ellesmere Island (76-82°N). Axel-Heiberg Island (79°25'N, 90°45'W). Baffin Island. Southampton Island. Manitoba. Umiat, Alaska. Payne River (59°30'N), Quebec.

*Pardosa glacialis* appears to be a nearctic species only.

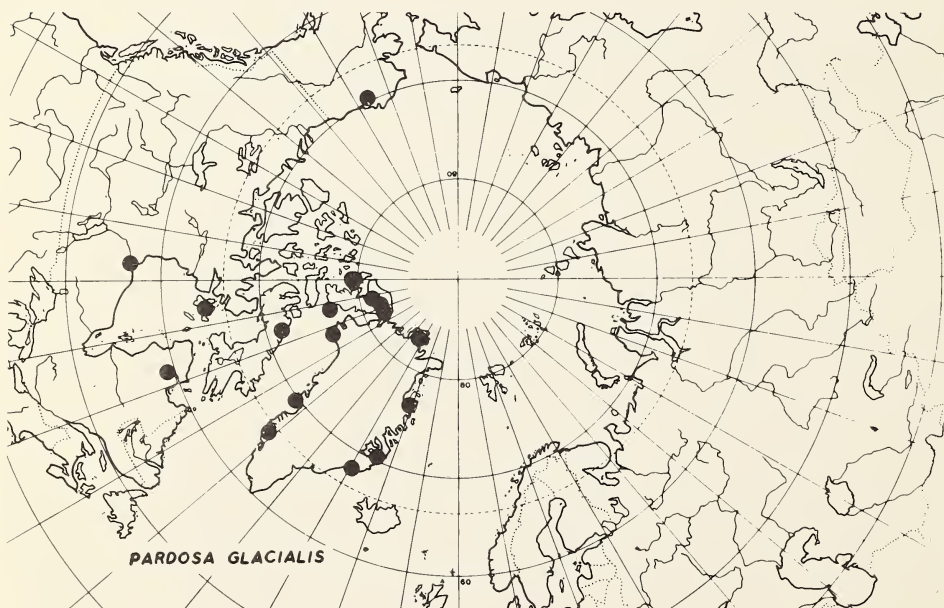


Fig. 10. Distribution map of *Pardosa glacialis*.

*Tarentula exasperans* Pickard-Cambridge, 1877, p. 283; (Figs. 35-37)

*Arctosa exasperans*: Bonnet 1955 p. 647; *T. exasperans*: Oliver 1963 p. 176, Braendegaard 1960 p. 8.

*Notes on taxonomy* - There has been some confusion about the classification of this species, mainly because of the scarcity of specimens in museums. Gertsch (1934) and Braendegaard (1960) have correctly replaced this species in the genus *Tarentula*.

*Description* - Braendegaard (1960, p. 10) has described the female of this species and has measured the sizes of a male and a female. I have remeasured a Peary Land specimen and a number of the Hazen Camp specimens, and find Braendegaard's measurements a little more than half of mine. Table 1 shows the measurements of individuals of this species from Hazen Camp.

TABLE 1 - Mean dimensions of *Tarentula exasperans* in mm.

	Carapace		Total Length
	Length	Width	
♂ (20 specimens)	3.35	2.76	7.06
♀ (10 specimens)	3.78	2.96	8.73

*Natural history* - This species is a member of the arid arctic faunal element, and is the most pronounced heliophile of all the species found at Hazen Camp. *T. exasperans* was taken only on dry southwest and south-facing slopes (rarely on southeast-facing) in and near clumps of *Dryas integrifolia*. Where this species is abundant, *P. glacialis* was almost never found except for occasional wandering males. *T. exasperans* overwinters by burrowing about 2.5 cm into the ground at the bases of *Dryas integrifolia*. It was never found in the night shadow areas or areas of slopes of more than 20°.

Figure 11 shows the main period of activity of the males and females of this species. The females are never as active in wandering as the males. Sexual activity of the males is between June 28 and July 6, though they can be found before and after these dates. The adults are not known to overwinter.

Newly emerged males and females were collected on the day they emerged, and then kept in separate cages for one week. On June 29, 1964, a male was introduced to a cage containing four females. Upon contact with a female, the male seemed to become excited. There was a short sparring contact, then each fled in different directions. The female went for about 5 cm and stopped, but the male began running about in small circles and figure-eights as though injured, with the front two pairs of legs drawn up against the carapace. Upon each contact with a female, the scurrings were intensified.



On June 30, 1964, two males and two females were placed in a large cage outside. On July 5, the males began courting the females. In all, five males were observed courting females, and there were no obvious differences. In this pattern of courtship the male approached the female, and at contact became more active and began circling and scurrying. Thereafter, the male approached the female almost invariably from behind, and tapped the female on the opisthosoma or fourth leg with his first legs. The female merely lifted a leg, and the male scurried off, but quickly returned and tried again. On the ninth or tenth try, the male retired for about five minutes.

The above procedures were watched for over five hours continuously, but no males were successful at mounting a female. The males were found dead the following morning. There was no mating observed for this species, nor even any partial attempts at mounting.

On July 6, 1964, a female and egg sac appeared in the outside cage. The process for egg-laying is as follows. The female *T. exasperans* laid eggs and made the egg sac in much the same way as *Pardosa glacialis* (see p. 165). The difference was that *T. exasperans* dug a hole in the ground about 2 cm deep and at the bottom of the hole made a round cavity about 1 cm in diameter. Once in the hole, the female closed over the entrance with webbing. The hole was completely lined with silk. The whole process, including the hole digging, took about four hours, but the female often remained inside the hole for another three to six hours. When the female emerged, the light brown egg sac was attached to the spinnerets. The egg sacs were larger and rounder than those of *Pardosa glacialis*. There are about 70 eggs per sac of *T. exasperans*. There is no great size difference between egg sacs.

The young were never observed clustered on the opisthosoma of the female as were the young of *P. glacialis*. About 204 specimens of various instars were examined to determine the number of instars and length of life cycle. The results were poor, mainly because there were a great many adults and penultimates, but very few of the preceding instars. However, by inspection, it appears that there may be as many as seven or eight instars, and a life cycle that may last six or seven years, if it is assumed that each instar lasts about one year.

No escape orientation was observed in *Tarentula exasperans* males or females, as the species relies on cryptic colouration rather than speedy retreats to elude enemies and predators. The gray and black colouration makes individuals almost invisible when they are in or near the dead leaves of *Dryas integrifolia*. Specimens observed in the field did not run at my approach but remained still. Even when the ground was shaken under them, they moved only if their positions were somewhat precarious.

It was found by experiment that this species prefers the smaller Diptera so abundant at Hazen Camp, though Collembola will be eaten if caught. Small blow flies (*Phormia* and *Protocalliphora* spp.) were refused even when the wings were cut off, perhaps because *T. exasperans* has very small chelicerae for a spider of its size. No parasites or predators of this species were observed, nor was cannibalism seen.

*Material examined* - About 397 adults of this species were examined

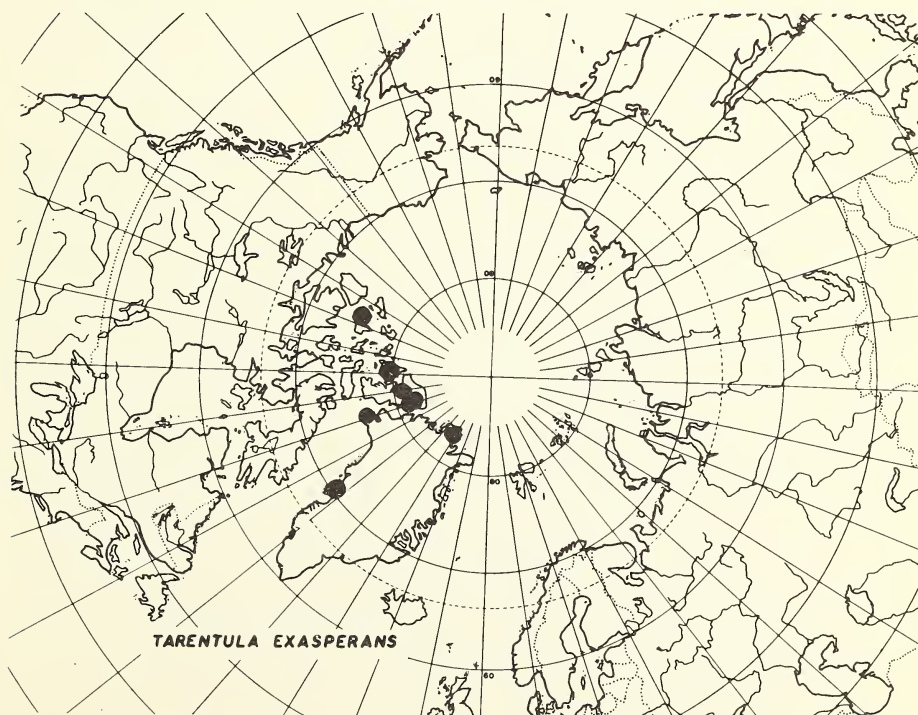
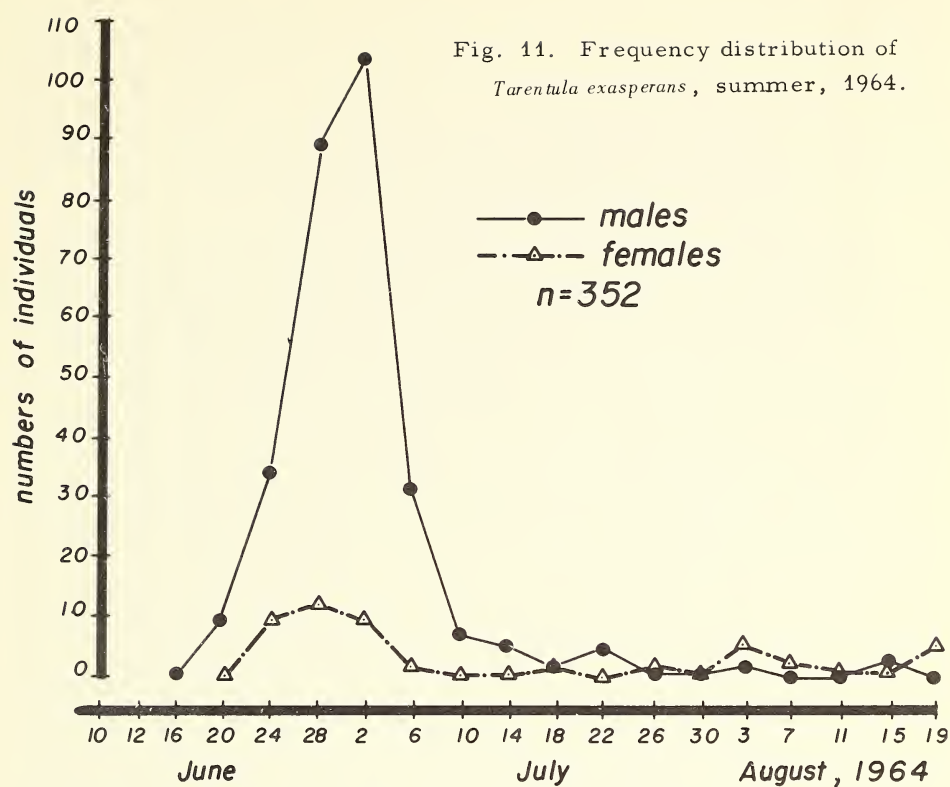


Fig. 12. Distribution map of *Tarentula exasperans*.

from Hazen Camp, one male from Peary Land, Greenland, which was loaned by the Zoological Institute in Copenhagen, three females and one male from Umanak, Greenland, loaned by the American Museum of Natural History, New York, one male and seven immatures from Tanquary Fjord, Ellesmere Island, 10 immatures from Axel-Heiberg Island (Heinz Rutz, collector, 1963), and three males and 34 immatures from Melville Island (J. E. H. Martin, collector, 1965).

*Distribution* (fig. 12) - Greenland (Peary Land; Umanak,  $70^{\circ}40'N$ ; Saunders Island,  $76^{\circ}35'N$ ,  $69^{\circ}45'W$ ). Ellesmere Island (Discovery Harbour,  $81^{\circ}45'N$ ; Hazen Camp; Tanquary Fjord,  $81^{\circ}28'N$ ,  $76^{\circ}50'W$ ). Axel-Heiberg Island. Melville Island ( $74^{\circ}58'N$ ,  $115^{\circ}00'W$ ). This species is known only from the high Nearctic Region.

### Linyphiidae

*Collinsia spetsbergensis* (Thorell) 1872 (Figs. 65, 69)

*Erigone spetsbergensis* Thorell 1872 p. 692. *Typhochraestus spitsbergensis*: Bonnet 1959 p. 4747, *C. spetsbergensis*: Holm 1960b p. 512; *C. spitsbergensis*: Braendegaard 1960 p. 11.

*Notes on taxonomy* - According to Åke Holm (pers. comm. 1965), Thorell's paper (1872) was written in Swedish, and since Spetsbergen is Swedish and Spitzbergen is German, the spelling *spetsbergensis* must stand as valid, despite Bonnet's (1955, p. 74; 1959, p. 4747) comment to the contrary.

*Description* - Female. Color: carapace brown, marked and shaded with dark brown; chelicerae pale yellow-brown with brown specks on the basal half; sternum brownish; labium brown, rimmed with gray; pedipalpcoxae brownish, gnathobases pale gray, abdomen gray-brown; spinnerets gray-brown.

Structure: size, moderately small, about 2.25 mm long; carapace distinctly longer than wide, about 0.86 mm x 0.69 mm, gradually rising to the cephalic region, then sloping downward to the eyes; cephalic lobe lacking; clypeus height about 3.5 to 4.0 diameters of an anterior median eye; posterior row of eyes slightly procurved; posterior medians slightly smaller than the laterals and all about equally spaced at 2.0 diameters of one median; anterior row almost straight, but slightly recurved; anterior medians slightly more than 2.0 diameters of one from the laterals; median ocular quadrangle longer than wide and wider posteriorly; promargin of cheliceral fang groove armed with five stout teeth; chelicerae slightly reclined; legs moderately long.

Tibiae I-III each with two spines; tibia IV with one spine at 0.41; trichobothrium (Tm) I about 0.64; Tm II about 0.61; Tm III about 0.46; Tm IV lacking.

Male. Color and structure: like those of the female, except for the following: total length about 2.0 mm; carapace longer than wide, about 0.80 mm x 0.74 mm.

Tibia I-III with two spines; tibia IV with one spine; Tm I about 0.56; Tm II about 0.50; Tm III about 0.47 or 0.48; Tm IV lacking,



*Natural history* - This species is a member of the humid arctic faunal element (Braendegaard 1946). Specimens are usually found in river deltas in areas with fine, muddy sand covered with dense *Equisetum* and some *Salix*. These areas are always very wet or damp, and are occasionally flooded in the spring. If the ground begins to crack with dryness, then *C. spetsbergensis* retreats into these cracks.

The adults are found throughout the season, though there is a slight increase of captured adults at the end. The species overwinters at the bases of the vegetation but not, so far as is known, as adults.

No parasites or predators were observed preying on this species, but it can be assumed that the young are eaten by other species and by their own adults.

*Material examined* - About 22 adults were examined from the Hazen Camp material, two females from Marie Bay, Bathurst Island (Leonard Hills, collector, summer, 1964), three females and two males from Bailey Pt., Melville Island (J. E. H. Martin, collector, 1965), 164 adults from Weatherhall Bay, Melville Island (Larry Law, collector, summer, 1964), one male from Isachsen, Ellef Ringnes Island (J. F. McAlpine, collector, 1960), two females from Alert, Ellesmere Island (personal collection, 1963) and four males and 17 females from Axel-Heiberg Island (Heinz Rutz, collector, 1963).

*Distribution* (fig. 13) - Alaska (Arctic Coast). Marie Bay, Bathurst Island. Weatherhall Bay and Bailey Point, Melville Island. Hazen Camp and Alert, Ellesmere Island. Isachsen, Ellef Ringnes Island. Greenland (Peary Land; E. Greenland, 62-65°N; W. Greenland, 70°N). Iceland. Spitsbergen. Sweden. Novaya Zemlya. Siberia. New Siberian Islands. This species is high Holarctic in distribution.

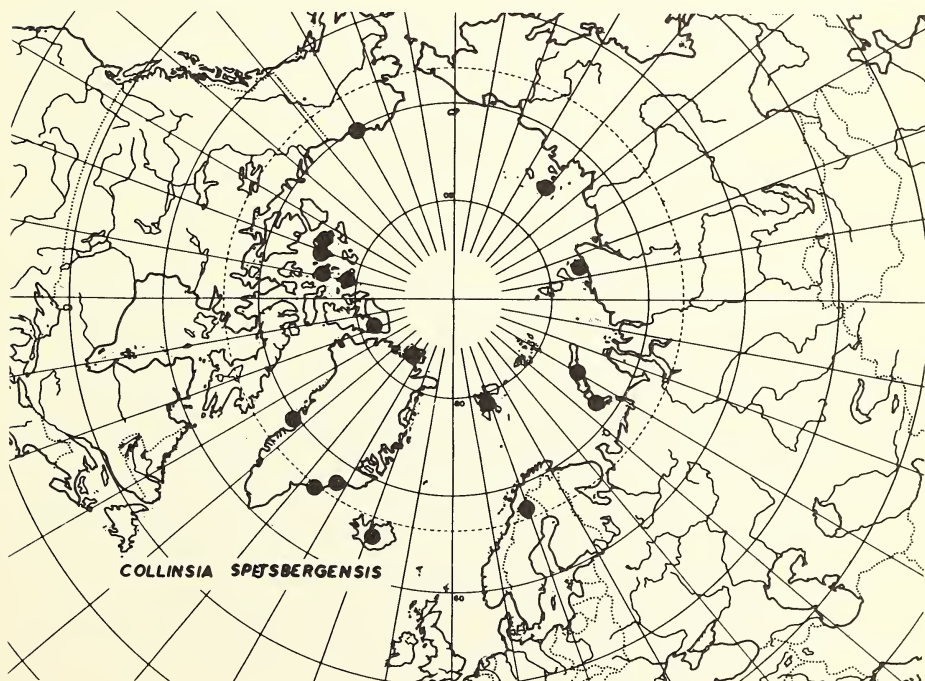


Fig. 13. Distribution map of *Collinsia spetsbergensis*.



*Collinsia thulensis* (Jackson) 1934, p. 614 (Figs. 66-68)

*Coryphaeolanus thulensis* Jackson 1934 pp. 614, 615, 618; *C. thulensis*: Bonnet 1956 p. 1231. *Collinsia thulensis*: Holm 1958a p. 48; b p. 531, 1960a p. 112; Braendegaard 1960 p. 12.

*Natural history* - This species is a member of the humid arctic faunal element. Specimens are most commonly found in gravelly parts of river deltas with scanty vegetation, mostly *Dryas integrifolia* and *Salix arctica*. *C. thulensis*, in contrast to *C. spitsbergensis*, is active mostly during the early part of the season. Overwintering forms were not found, but it appears from the habitat that the species overwinters on the surface of the ground, perhaps under some of the stones or in the vegetation.

The active breeding period is indicated in figure 14. Note the low number of adults caught at the end of the season. From this I assume that the adults do not overwinter.

Captured specimens kept in cages fed readily on mites and Collembola, but refused all flies offered, including very small Ceratopogonidae.

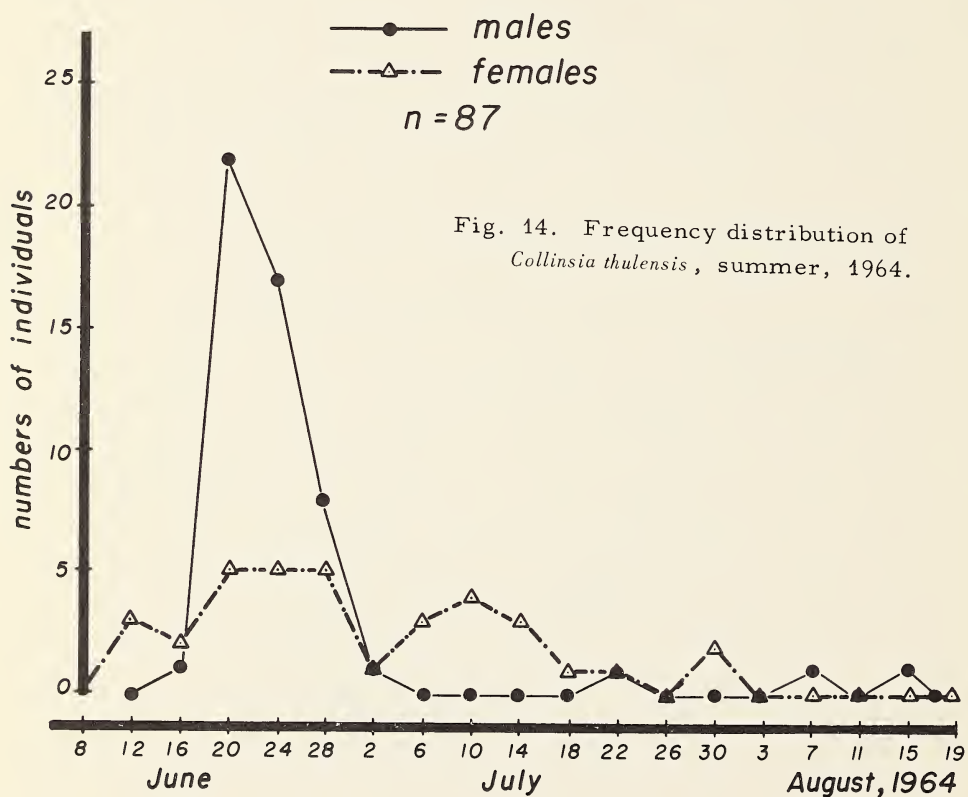


Fig. 14. Frequency distribution of *Collinsia thulensis*, summer, 1964.

*Material examined* - About 100 adults of this species were examined from Hazen Camp, six females and one male from Thule, Greenland (personal collection 1964), and one female from Axel-Heiberg Island (Heinz Rutz, collector, 1963).

*Distribution* (fig. 15) - Kotzebue, Alaska. Hazen Camp, Ellesmere Island. Axel-Heiberg Island. Greenland (Thule; Peary Land; and between 70-75°N in E. Greenland). Spitsbergen.

This species appears to have an Holarctic distribution.

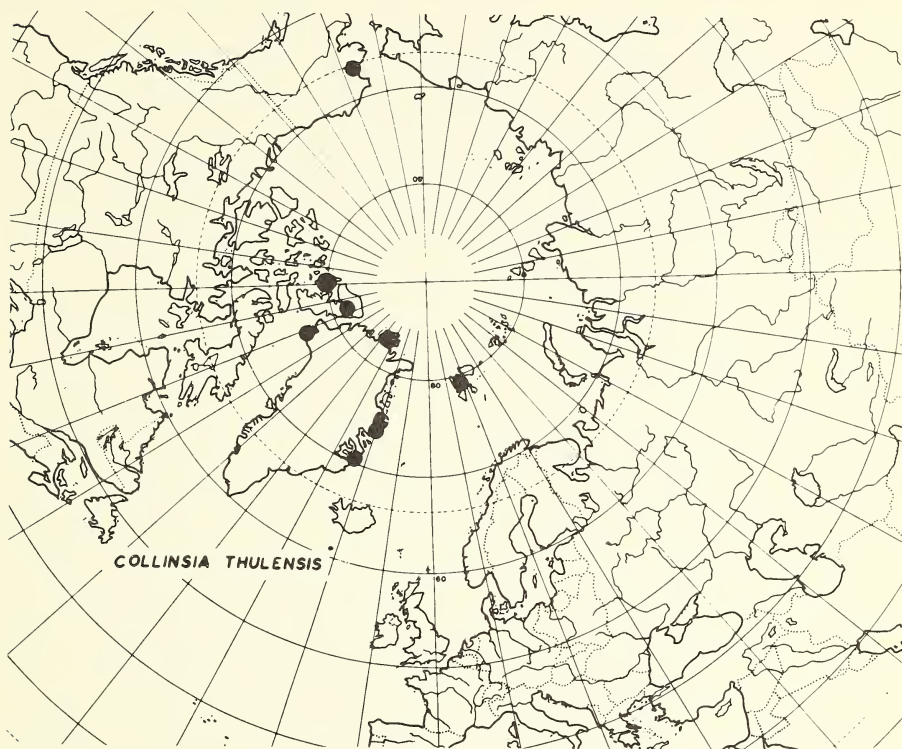


Fig. 15. Distribution map of *Collinsia thulensis*.

\* *Cornicularia karpinskii* (Pickard-Cambridge) 1873, p. 447 (Figs. 51-53)

*Erigone karpinskii* Pickard-Cambridge 1873 p. 447; *C. karpinskii*: Bonnet 1956 p. 1223; Holm 1960a p. 113, b p. 513.

*Notes on taxonomy* - As suggested by Holm (1958a), *C. karpinskii* seems to be a complex of species whose components are not understood, or else this is a polytypic species. None of the 30 males examined showed any variation in the tibial apophysis, a feature that is variable in some other populations of this species (Holm 1958a, pp. 53, 54). The only observed variable feature in this species was the two lobes of the epigynum, whose proportions of length and width varied slightly.

\* Examinations of the holotype of *Cornicularia clavicornis* Emerton (1882, Trans. Conn. Acad. Arts Sci. 6 : 1-86) shows that the Lake Hazen material should be referred to this species. Details will be published later.

*Description* - Male. Color: carapace pale yellow-brown; eyes ringed with dark brown; legs pale yellow; opisthosoma pale gray-green with four red-yellow spots on the dorsum; sternum golden brown with brown margin; chelicerae golden brown; labium pale brown with gray margin.

Structure: size medium small, entire length about 2.31 mm; carapace distinctly elongate, 0.96 mm long x 0.72 mm wide; carapace gradually rising to the head part, dropping forward and down to the anterior median from the posterior median eyes, then the clypeus drops vertically from the anterior medians; horn placed midway between the anterior and posterior medians, projecting forward and upward, barely, if at all, extending beyond the vertical face of the clypeus; horn with a greater diameter distally than basally; height of clypeus about 3.5 to 4.0 diameters of an anterior median eye; chelicerae vertical or nearly so, perhaps slightly reclined; stridulation organ on lateral sides of chelicerae distinct; eyes equal or subequal in size; posterior row decidedly procurved and all eyes equally spaced at about 1.8 diameters of one posterior median; anterior medians about 0.20 diameters of one apart, and about 0.80 diameters of one from the laterals.

Sternum longer than wide and with a sparse cover of thin hairs; legs not strikingly long or short; tarsal claws with a full complement of teeth, and resembling a comb; the two tibial apophyses of the pedipalp elongate and projecting forward and down atop the cymbium; median apophysis curving down and forward under the lateral, then continuing parallel but ventral to it; median apophysis bifid terminally, one broad, flat, lateral projection with blunt spines pointing outward below and beyond the lateral apophysis, and the other pointed and running parallel to the terminal part of the lateral apophysis; the lateral apophysis curved slightly to the median line, then turned outward at the terminal one-third, ending in a blunt point; the embolus and other parts of the tarsus within the cymbium as in figure 52. Anterior margin of the opisthosoma protruding over the carapace; four small, pale red-yellow depressions on the dorsum of the opisthosoma, the anterior pair closer together than the posterior; average of five measurements of the opisthosoma is 1.35 mm.

Tibia I-II with two spines; tibiae III-IV with one spine each at 0.20 and 0.19 respectively; Tm I about 0.53; Tm II about 0.50; Tm III about 0.47; and Tm IV about 0.31.

Female. Color and structure: Like the male except that the horn is lacking; average length of five females is about 2.55 mm, carapace 0.93 mm, and the opisthosoma about 1.60 mm; tibiae I-III with two spines; tibiae IV with one spine at 0.16 to 0.17; Tm I about 0.46-0.47; Tm II about 0.46 to 0.47; Tm III about 0.47; Tm IV about 0.50.

*Natural history* - This species is a member of the humid arctic faunal element. It lives in the cracks in the ground and ventures onto the ground surface only when the relative humidity is above 90%. The soil is calcareous with sparse vegetation. The adults and young were found deep in the cracks in the ground where the relative humidity approached 100%. No overwintering sites were found, but I assume that individuals overwinter fairly close to the ground surface.

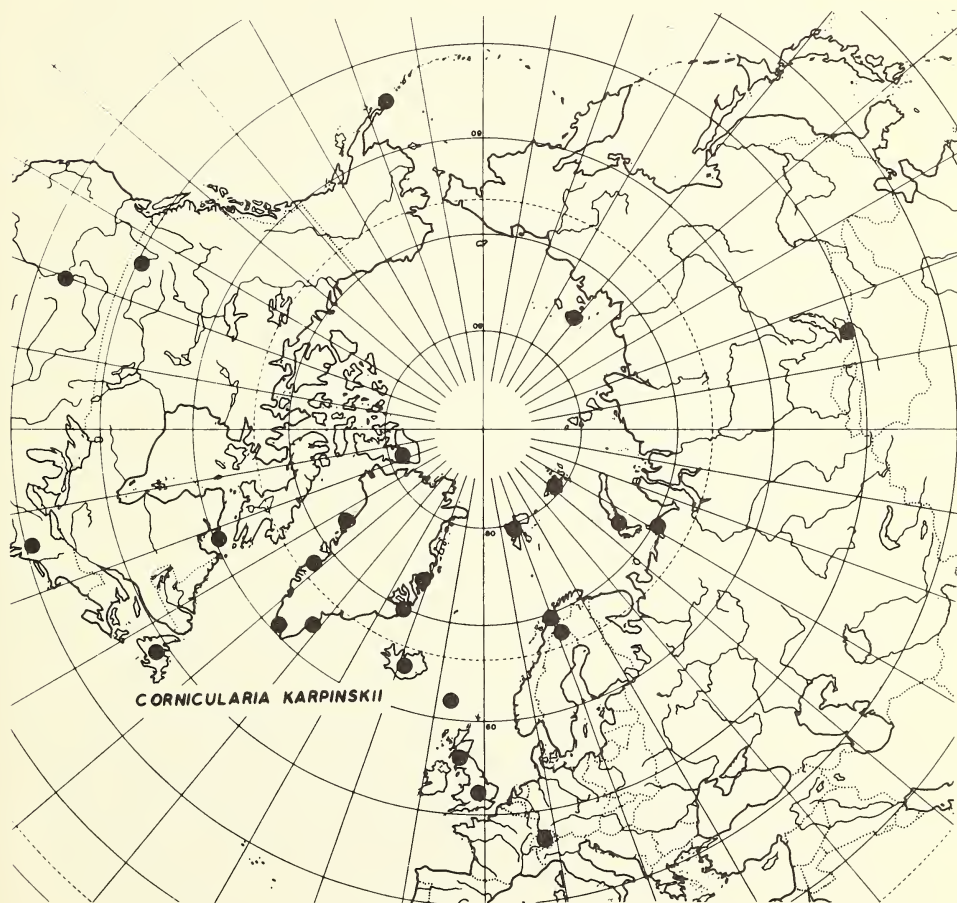
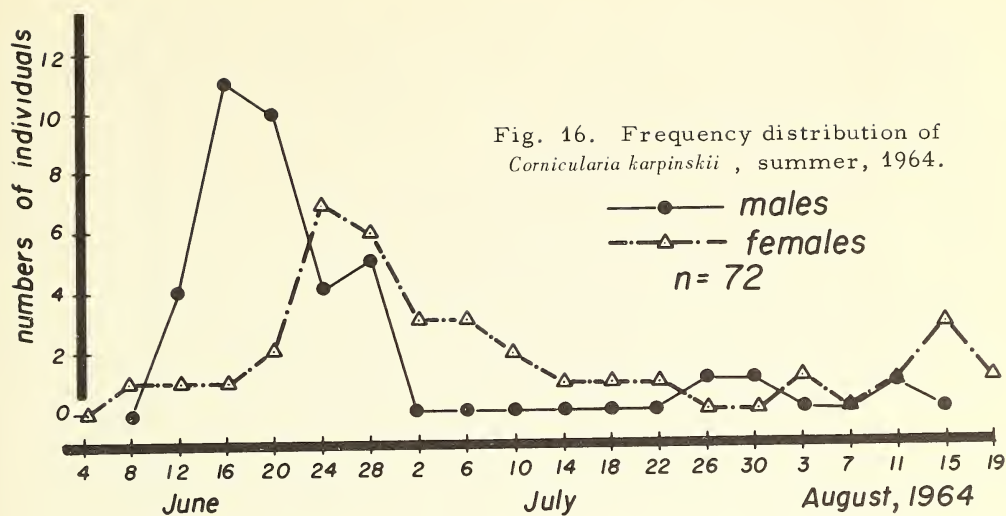


Fig. 17. Distribution map of *Cornicularia karpinskii*.



Figure 16 shows the frequency distribution of this species during the summer of 1964. There are no comparable data from 1963. *C. karpinskii* appears to be able to overwinter in the adult stage, as adults were caught before the spring melt. No parasites or predators were found for this species.

*Material examined* - About 78 specimens of this species were examined from Hazen Camp, and two from the Aleutian Islands, Alaska.

*Distribution* (fig. 17) - Unalaska Island and Umnak Island, Alaska. Banff, Alberta. Yellowstone Park, Wyoming. New York. Newfoundland. Akpatok Island, Ungava Bay, N. W. T. Lake Hazen, Ellesmere Island. East and West Greenland. Iceland. The Faeroes. England and Scotland. The Swiss Alps. Northern Scandinavia. Spitsbergen. Franz Joseph Land. Novaya Zemlya. Waigatsch Island. Lake Baikal, Siberia. Kamchatka.

This species is circumpolar in distribution, though, as mentioned in the notes on taxonomy, it is not certain that this distribution represents only one species.

*Erigone psychrophila* Thorell, 1872 a p. 689 (Figs. 42-44)

*E. psychrophila*: Bonnet 1956 p. 1772; Holm 1958a p. 52, b p. 532, 1960a p. 116, b p. 513; Braendegaard 1960 p. 12; Oliver 1963 p. 176.

*Natural history* - This species is a member of the humid arctic faunal element. *Erigone psychrophila* is restricted to vegetated, marshy areas at the edges of ponds and quiet streams and to water-saturated, vegetated slopes. These data do not quite agree with Holm (1958a, p. 53) who states that *E. psychrophila* belongs to both the dry and humid faunae. The species apparently overwinters in the vegetation and can often be found moving under water in the slush snow during the spring melt.

Figure 18 shows the main activity period and summer distribution in numbers. The males are very active during the mating season, then are scarce thereafter. The sharp drop in the number of females caught in early July can be attributed mostly to the females secluding themselves while egg laying. The drop-off in early August might be attributed to death of the females and to inactivity because of cool weather. The adults are apparently able to overwinter as they are found at the very beginning of the season.

No parasites or predators of this species were found, but I assume that as in the case of all these small spiders, they are prey to the larger spiders.

*Material examined* - About 1983 adult specimens of this species were examined from Hazen Camp, nine females, three males and six immatures from Cornwallis Island (Leonard Hills, collector, 1964), one male from Thule, Greenland (personal collection, 1964), 355 adult specimens from Melville Island (Larry Law, collector, 1964), and one male, one female and one immature from Mould Bay, Prince Patrick Island (J. E. H. Martin, collector, 1965).

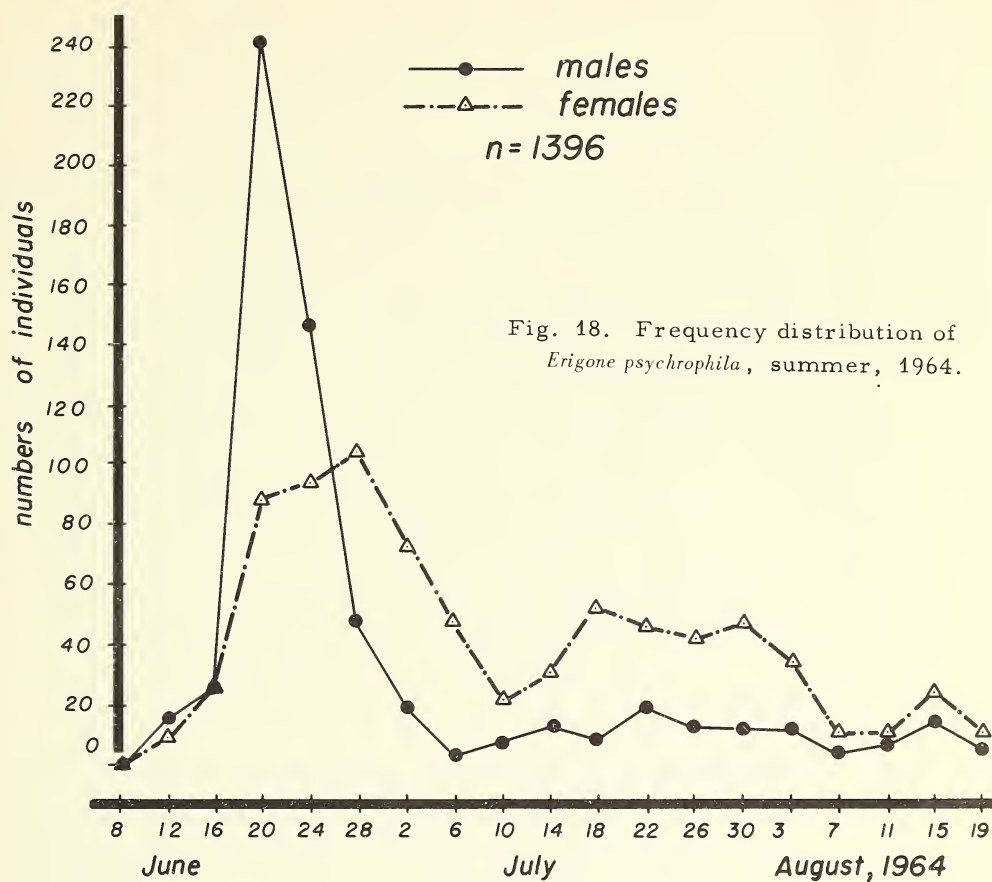


Fig. 18. Frequency distribution of *Erigone psychrophila*, summer, 1964.

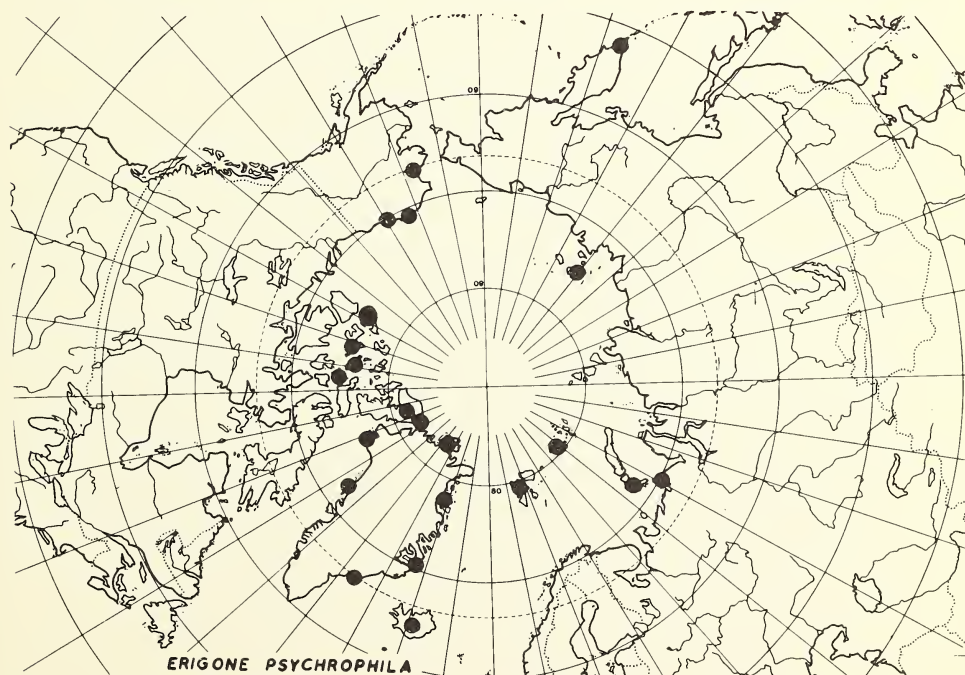


Fig. 19. Distribution map of *Erigone psychrophila*.

*Distribution* (fig. 19) - Coastal Alaska (Arctic and Bering). Weather-hall Bay, 75°46'N, 106°56'W), Melville Island. Mould Bay, Prince Patrick Island. Marie Bay, Bathurst Island. Cornwallis Island. Alert and Hazen-Camp, Ellesmere Island. Greenland (Peary Land; East Greenland, 67-77°N; West Greenland, 74-77°N). Iceland. Spitsbergen. Northern Scandinavia. Novaya Zemlya. Waigatsch Island. Franz Joseph Land. New Siberian Islands. Kamchatka. This species is circumpolar in distribution.

*Hilaira vexatrix* (Pickard-Cambridge) 1877, p. 280 (Figs. 15, 16)

*Erigone vexatrix* Pickard-Cambridge 1877 p. 280. *Hilaira vexatrix*: Bonnet 1957 p. 2214; Holm 1958b p. 532; Braendegaard 1960 p. 14.

*Notes on taxonomy* - Schenkel (1950) lists a record of this species from Banff, Alberta. Without seeing the Alberta specimens, I cannot agree that this species has anything but a high arctic distribution. Holm (1956) does not list Schenkel's reference, nor does he give any comment about an Alberta record. All previous records for this species are above 70°N latitude.

*Natural history* - This species is a member of the humid arctic faunal element, as it is found only in damp, vegetated regions that are rarely, if ever, inundated. Many specimens were collected in the damp, upper edges of ponds and small streams that have dense vegetation and many rocks under which they may crawl to overwinter. Specimens of *Hilaira vexatrix* overwinter under rocks and in cracks in the ground about one to two cm deep. They are active on the ground as soon as the ground temperature is above freezing, even though the air temperature is well below freezing.

Figure 20 shows the activity periods of this species during the summer. The June 16 to 24 peak is the period of courting and mating, and the peak at the end of the season is the increase of adults that will overwinter. Therefore, the peaks belong to two distinct populations of adults. The adults of this species overwinter.

Neither courtship nor mating were observed in this species; the males died about five days after mating.

On June 15, 1964, two females laid eggs which were in small, lenticular, white egg sacs. On June 18, a third female laid eggs. The egg sacs were suspended in tangle webs about one cm above the ground. The females remained with the eggs until after the young had emerged. One of the females ate the male after mating.

On July 3, the small spiders were visible inside the egg sacs, and on July 12, the young from the eggs laid on June 15 emerged. On July 20, the young from the third sac emerged. The three sacs contained 9, 11, and 8 eggs respectively. The egg sacs were kept at a constant 100% relative humidity.

The females did not feed and were not fed for a period of six weeks, and at the end of this period showed no signs of stress. Collembola were introduced as food, but the females showed no interest. All three females were dead by August 10.

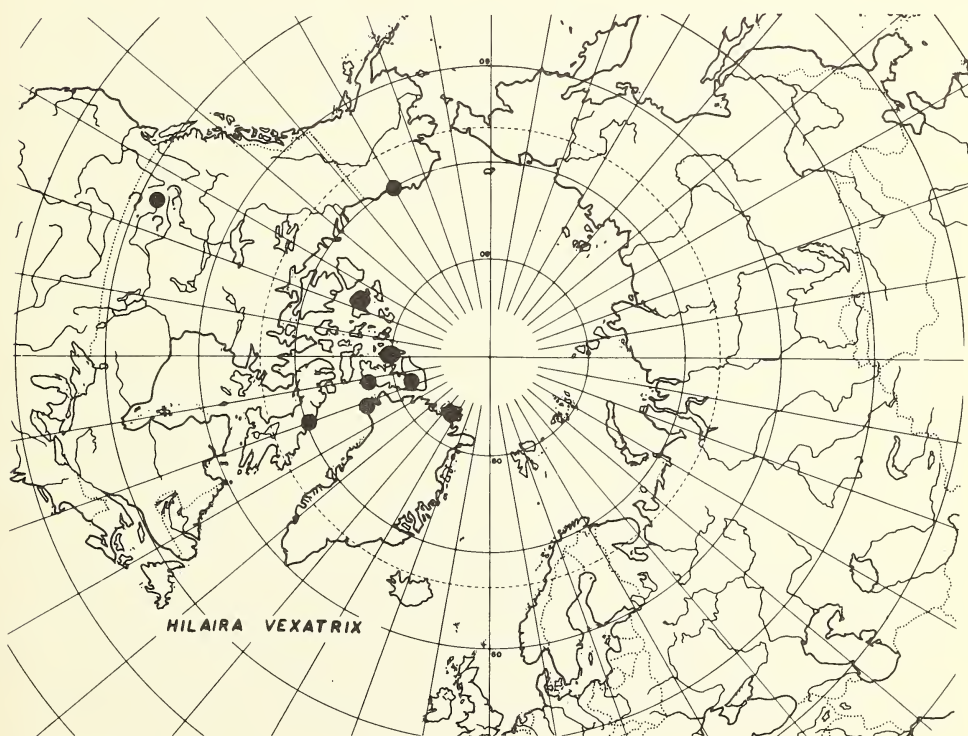
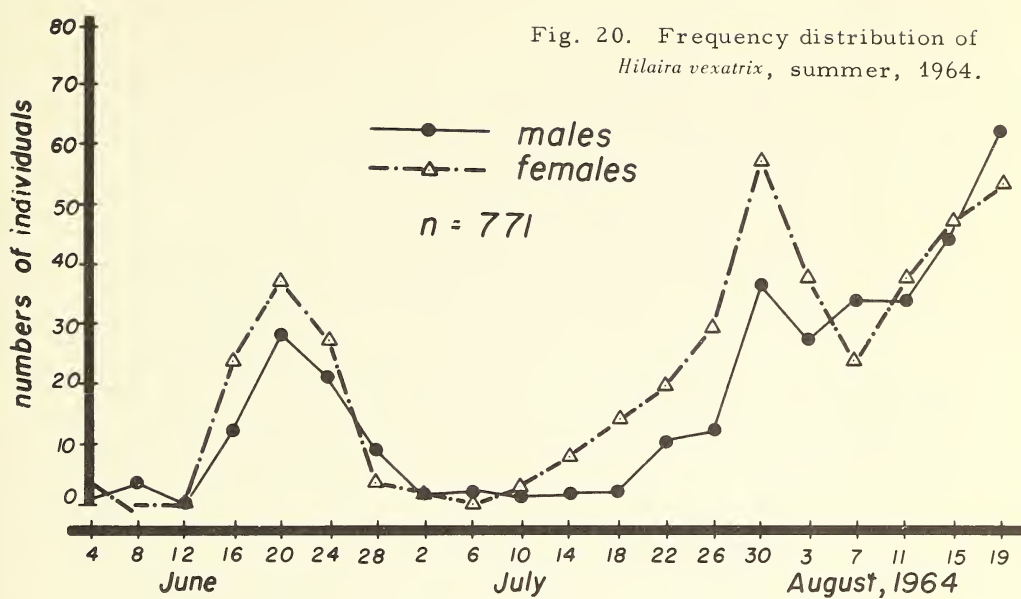


Fig. 21. Distribution map of *Hilaira vexatrix*.



No parasites or predators of this species were found. A great number of the immatures die by cannibalism.

*Material examined* - About 2159 adults of this species were examined from Hazen Camp, two males and eighteen females from Thule, Greenland (personal collection, 1964) 63 males and 91 females from Axel-Heiberg Island (Heinz Rutz, collector, 1963), and one male, 18 females and 17 immatures from Melville Island (J. E. H. Martin, collector, 1965).

*Distribution* (fig. 24) - Greenland (Peary Land; Thule). Ellesmere Island (Alert; Hazen Camp; Discovery Harbour). N. E. Coast of Baffin Island. Axel-Heiberg Island. Melville Island. Arctic Coast of Alaska. Banff, Alberta (?).

This species is Nearctic. The chances of it being found in the Palearctic Region are slight, as Braendegaard (1958) has studied the Iceland material, Locket and Millidge (1951, 1953) have studied the British material and Wiehle (1956, 1960) has studied the German material.

\* *Meioneta nigripes* (Simon) 1884, p. 439 (Figs. 62-64)

*Microneta nigripes* Simon 1884 p. 439. *Meioneta nigripes* Bonnet 1957 p. 2756; Braendegaard 1958 p. 80, 1960 p. 15; Holm 1958a p. 56, 1960 b p. 513.

*Natural history* - This species is a member of the humid arctic faunal element. Individuals live deep in soil cracks or under medium to large-sized stones on very dry south- to southwest-facing slopes. That is, the macroclimatic conditions are dry, but the microclimatic conditions are humid. Braendegaard (1946, 1960) considers this species to be euryoecious (euryecious), but examination of the microclimate leaves no doubt that it is a humid arctic species.

Overwintered adults were collected on June 1, 1964, before the spring thaw. Inactive females were collected from under rocks that were frozen to the ground surface. These females became active within ten seconds of the time they were collected and exposed to the sun. Figure 22 shows the peak of activity for the species at the beginning of the season.

Courtship was observed in several pairs of this species and no variation was seen. Observations were started on June 1, 1964. Males and females were placed in a small bottle with soil and rocks. Random wandering was observed for several hours, after which time the males selected areas that they would mildly defend. These were small areas in which each male had built a small, horizontal, almost invisibly-thin sheet web about 2 x 4 mm, and from which the males hung upside down. Each male remained on this sheet for about 15 minutes. These were, I believe, the sperm webs, though no sperm droplets were seen. Eventually, each male searched for and built a small tangle web near a female. When the web was built, each male began a combination of activities as follows: each palpus was jerked forward and back alternately, much like two pistons. At the same time, the whole body was jerked back and forth. Coordinated with these was a gradual approach towards the female. About three mm from the female, the male began body-jerking and strumming one front foot, then the other. Then the female started the same sort of

\* Examinations of the holotype of *Meioneta maritima* (Emerton) New combination (1919, Rep. Can. Artic Expedition 1913-18, 3 : 4H) shows that the Lake Hazen material should be referred to this species.

motions. When their front legs touched, the female fled with the male in jerky pursuit.

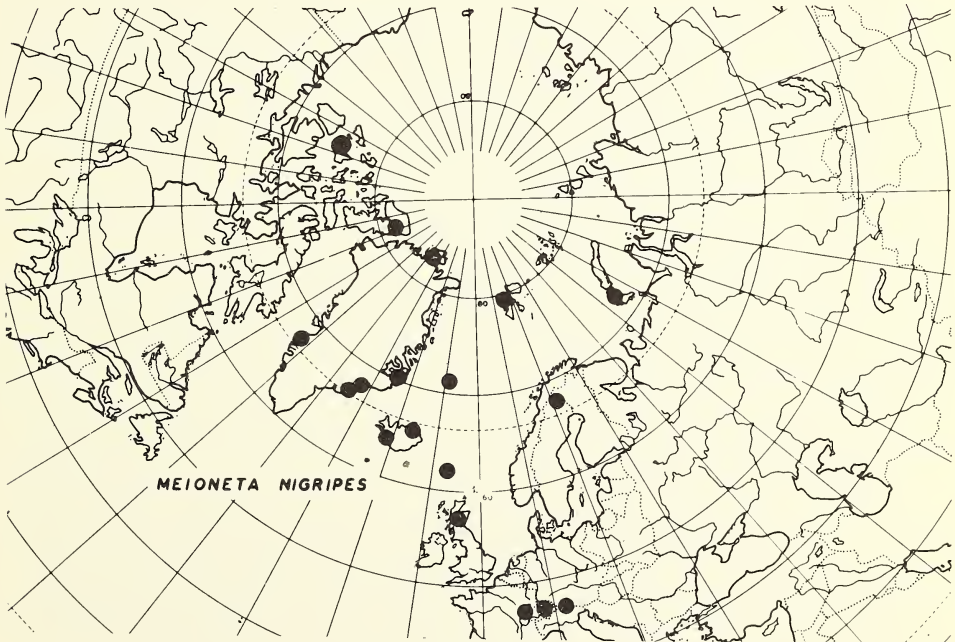
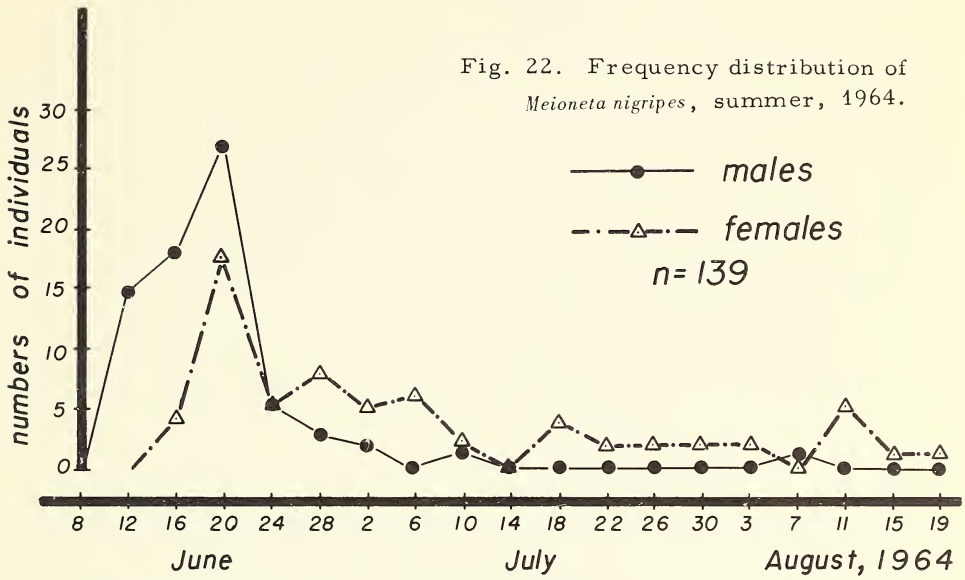


Fig. 23. Distribution map of *Meioneta nigripes*.

During the next 45 minutes, the males and females engaged their front legs for brief moments, then broke contact. At 90 minutes, one of the females built a small tangle and sheet web, then hid in one corner of the web. In a few minutes, the female was found by the male. The male began improving the web and the two finished the preparations in eight minutes. The web was made while both were upside down.

At this point the male and female stopped and remained still for five minutes. Gradually, with increasing vigour, the male began jerking in the web, and shortly after the female began strumming. Slowly, the male stopped jerking and began strumming, and approached the female as he did so. Then the palpi began pushing back and forth like pistons. (Both spiders were still hanging upside down from the sheet web.) When their legs touched, the female did not scurry away, but relaxed the front two pairs of legs so that the prosoma hung down from the web.

In mating, the male came forward so that his carapace touched the sternum of the female. At the same time, the right palpus shot forward, grappled with the epigynum, and lifted part of it away. The haematodocha expanded and the embolus twisted spirally into the spermathecal duct. The right palpus was engaged for one second, then the left palpus was applied for the same length of time. During the next 18 min 25 sec the male alternated the palpi 380 times. At no time was the male held captive by the female.

The male left the female for 40 seconds and retired to a small corner of the web where possibly the sperm were replenished in the palpi. The male then rejoined the female and during the next 6 min 41 sec, alternated the palpi 150 times before again returning to the corner to replenish the sperm. Returning to the female, the male again alternated the palpi on the epigynum, but now more slowly. In 6 min, only 40 alternations; at 11 min, only 6 more times; and in the last 33 min, the palp were alternated 37 more times. The last 6 couplings took about two min each. The female effected the finish. Shortly thereafter, the two fled in opposite directions.

More pairs were observed mating. The females seemed to be eager to mate several times with any male and often tried, but no male could be persuaded to engage a female - any female - more than once.

Four days after mating on June 5, 1964 two females laid eggs in small, round, white egg sacs. The egg sacs were attached directly to the side of the container. As with *H. vexatrix*, the eggs were kept in 100% relative humidity. More eggs were laid by other females on July 12 and August 24.

On July 3, 1964, eight young emerged from each egg sac laid on June 5. During the development of the eggs, the females stayed within two to three cm of the eggs.

On July 12, Collembola were introduced to the females and young for food. The females fed immediately. I also observed that females captured and bit several Collembola, leaving them inactive in the tangle web about the egg sac, and later returned to feed on them. The young spiders appeared to be too small to feed on Collembola. Most of the young died by cannibalism. The females of this species refused to eat anything but Collembola and Acarina, even though they were offered

small Diptera and spiders. No parasites or predators of this species were found.

*Material examined* - About 157 adults of this species were examined from Hazen Camp, and one male and 13 females from Bailey Point, Melville Island (J.E. Martin, collector, 1965).

*Distribution* (fig. 23) - Ellesmere Island (Hazen Camp). Bailey Point, Melville Island. Greenland (Peary Land; W. Greenland at 63°N; E. Greenland from 63-70°N). Iceland. Spitsbergen. Jan Mayen Island. The Faeroes. Scotland. North Sweden. Novaya Zemlya. The French, Swiss, and Tyrolian Alps.

This species is mainly Palearctic in distribution, but the Hazen Camp record makes it Holarctic. Judging from the known distribution, it is likely to be found across the high Nearctic.

*Minyriolus pampia* Chamberlin, 1948, p. 539 (Figs. 47-50)

*M. pampia*: Oliver 1963 p. 176.

*Notes on taxonomy* - Previous to the collections made at Hazen Camp, this species was known only from one male from Clyde River, Baffin Island. In 1963 and 1964, about 520 males and females and an unknown number of immatures of this species were collected. I have redescribed the male and have provided illustrations. The female is here described and drawn for the first time.

*Description* - Female. Color: carapace brown, splotched and streaked with dark brown; chelicerae yellow-brown; sternum brown; labium brown, but rimmed with gray; coxae of pedipalpi yellow brown, but gray at the gnathobases; legs and pedipalpi yellowish brown, flecked with gray-black spots near the joints; opisthosoma ovate, pubescent, gray-black with fine green streaks and four small reddish spots on the dorsum; spinnerets brown.

Structure: carapace rounded, cephalic region slightly elevated; height of clypeus about 3.5 diameters of an anterior median eye; eyes small; posterior row slightly procurved; posterior medians about 2.0 diameters of one apart, and about 1.5 diameters of one from the posterior laterals; anterior row almost straight; anterior medians about half of an anterior lateral in size.

Anterior medians about one diameter apart, and each about 1.7 diameters from the anterior laterals; median ocular quadrangle longer than wide and wider behind than in front; chelicerae reclined; sternum only slightly longer than wide, and separating the hind coxae by almost the length of one.

Total body length  $1.85 \pm 0.15$  mm; carapace length  $0.62 \pm 0.03$  mm; carapace width  $0.59 \pm 0.02$  mm; legs moderately short, metatarsi slightly longer than tarsi; pedipalp tarsus lacking a spine or claw at the tip; metatarsi each bearing one long trichobothrium at 0.74 or 0.75; tibiae I-III with two spines, tibiae IV with one spine.

The color and structure of the male are like those of the female,



except for the following points. Total length  $1.59 \pm 0.11$  mm; carapace length  $0.63 \pm 0.01$  mm; carapace width  $0.61 \pm 0.02$  mm; tibiae I-III with two spines, tibiae IV with one spine; Tm IV at 0.78.

*Natural history* - This species is a member of the humid arctic faunal element. It was found only on densely-vegetated slopes which are permanently water-saturated, and which are south- and southwest-facing. It is further restricted to the night shadow area.

Figure 24 shows the main period of activity of the males of this species. I am not able to explain the higher peak of the females which coincides with the peak of the males. Adults apparently overwinter as they were found in the slush ice at spring melt. No parasites or predators of this species were observed.

*Material examined* - About 581 adults of this species were examined from Hazen Camp. The holotype was not seen.

*Distribution* (fig. 25) - This species is known only from Hazen Camp, Ellesmere Island, and River Clyde, N. E. Baffin Island, N. W. T., Canada ( $70^{\circ}\text{N}$ ,  $70^{\circ}\text{W}$ ).

*Savignya barbata* (Koch), 1879, p. 60 (Figs. 58-61)

*Erigone barbata* Koch 1879 p. 60. *Savignya barbata*: Roewer 1942 p. 623.

*Typhochraestus barbatus*: Bonnet 1959 p. 4745.

*Notes on taxonomy* - The spelling of the generic name should be "Savignya", not "Savignia". The genus was named after Jules César Savigny, a French biologist of the early 19th Century, by Blackwall (1833).

*Description* - Female. Color: carapace brown with dark brown markings; chelicerae pale yellow with a brownish tint; sternum dark brown; legs pale yellow-brown with small brown splotches; opisthosoma gray-black with four small pale gray to reddish spots on the dorsum; spinnerets brown; coxae brown, gnathobases gray; labium brown with gray trim.

Structure: size small, about 1.80 mm long; carapace broad and rounded, slightly longer than wide, 0.62 mm long x 0.57 mm wide; carapace raised behind the cephalic region, and sloping down to the eyes; one anterior median eye about 0.5 diameters of a lateral; anterior row in a straight line; anterior medians about two diameters of one from the laterals; posterior row slightly procurved; posterior medians slightly more than two diameters of one apart, and about two diameters of one from the laterals; posterior eyes equal or subequal in size; median ocular quadrangle wider posteriorly than anteriorly; posterior medians about as far apart as the quadrangle is long.

Chelicerae reclined; sternum wider than long, proportions are 2.1 : 1; legs moderately short; tibia I-II with two spines, tibia III-IV with one spine; Tm I about 0.52; Tm II about 0.46; Tm III about 0.42; Tm IV lacking.

The male is like the female in color and structure except for the

following features. Size small, about 1.68 mm long; carapace rounded, 0.62 mm long x 0.62 mm wide; carapace raised into a cephalic lobe; cephalic pits opening out to horizontal grooves that run posteriorly the full length of the cephalic lobe.

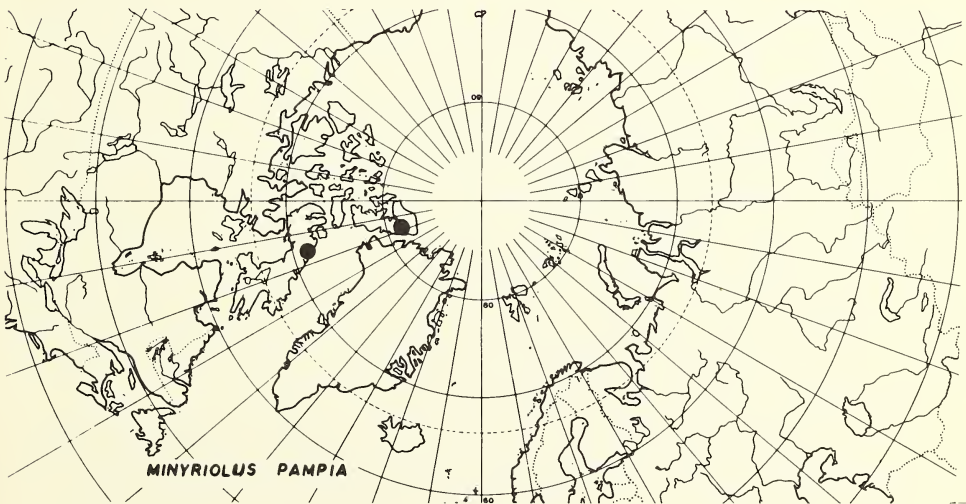
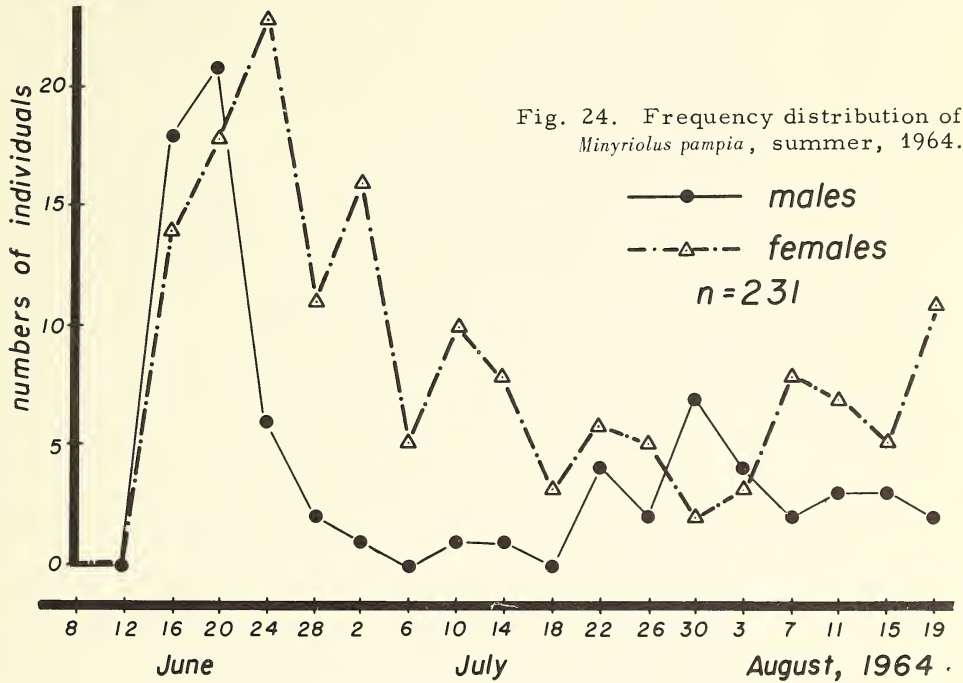


Fig. 25. Distribution map of *Minyriolus pampia*.

Eyes small; posterior row decidedly procurved; posterior medians at the top front edge of the cephalic lobe and almost five diameters of one from the laterals; laterals about two diameters of a median in size; anterior and posterior laterals on a small, common tubercle.

Clypeus height about ten diameters of an anterior median eye; clypeus pubescent with short, stiff, straight, pale-colored hairs; tibia I-II with two spines; tibia III-IV with one spine; Tm I about 0.58; Tm II about 0.54; Tm III about 0.50; Tm IV lacking.

*Natural history* - This species is a member of the humid arctic faunal element. It was found only in the gravelly sections of river deltas with scattered surface vegetation. The webs are built in the cracks in the ground and rarely on the surface. It appears to overwinter on or near the surface under rocks and in vegetation.

Figure 26 indicates the most active period of the summer season for the males. It is not known if the adults overwinter.

*Material examined* - About 100 adults of this species were examined from Hazen Camp, one female from Thule, Greenland (personal collection), two females from Bailey Point, Melville Island (J. E. H. Martin, collector, 1965), five males and five females from Weatherhall Bay, female from Axel-Heiberg Island (Heinz Rutz, collector, 1963).

*Distribution* (fig. 27) - Siberia (exact locality I could not find). Novaya Zemlya. Spitsbergen. Greenland (Etah, and Thule). Ellesmere Island (Hazen Camp). Melville Island. Axel-Heiberg Island. This species is Holarctic in distribution, but it is known only from the high arctic.

*Typhochraestus latithorax* (Strand), 1905 (Figs. 54-57)

*Tarsiphantes latithorax* Strand 1905 p. 23; *T. latithorax*: Bonnet 1959 p. 4262; *Typhochraestus latithorax*: Holm 1960b p. 511.

*Notes on taxonomy* - In 1905, Strand erected the new genus *Tarsiphantes*, with the one species, *latithorax*. The species was described from one damaged female and one subadult female. Holm (1960) synonymized *Tarsiphantes* Strand, 1905, as a junior synonym of *Typhochraestus* Simon, 1884, based on a study of the holotype of *latithorax*. The holotype had in the meantime become dried and even more damaged than when Strand described it.

The genus *Typhochraestus* is determined and defined by the characters of the palpus of the male, which has a large, spiral embolus with a small, somewhat spiral basal apophysis (see Holm 1943, and Wiehle 1960). The males of *latithorax*, here described and figured for the first time, have these features.

Strand reports (1905, p. 23) that "Diese neue Gattung, deren Type und einzige Art die neue *T. latithorax* Strand ist, . . . wurde am Rice Strait, 30/6 1898 entdeckt . . .". However, the ship "Fram" did not reach Rice Strait until at least August 17, 1898, so either the year or the month is in error. During June 1899, Dr. Johan Svenden, the "Fram's" doctor, did some collecting at Fort Juliana (79°03'N, 77°43'W). About August 12,

1899, the "Fram" left the Rice Strait for Payer Harbour, and later Jones Sound (Bryce 1910, p. 245). Thus, it is more likely that Fort Juliana is the actual collecting site for this species. Rice Strait ( $78^{\circ}34'N$ ,  $74^{\circ}45'W$ ) is close to Fort Juliana.

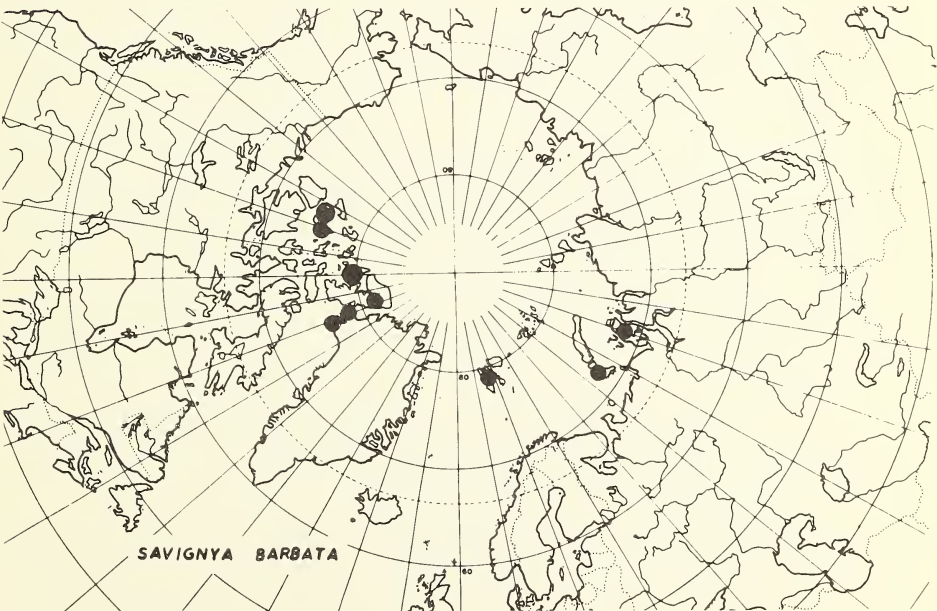
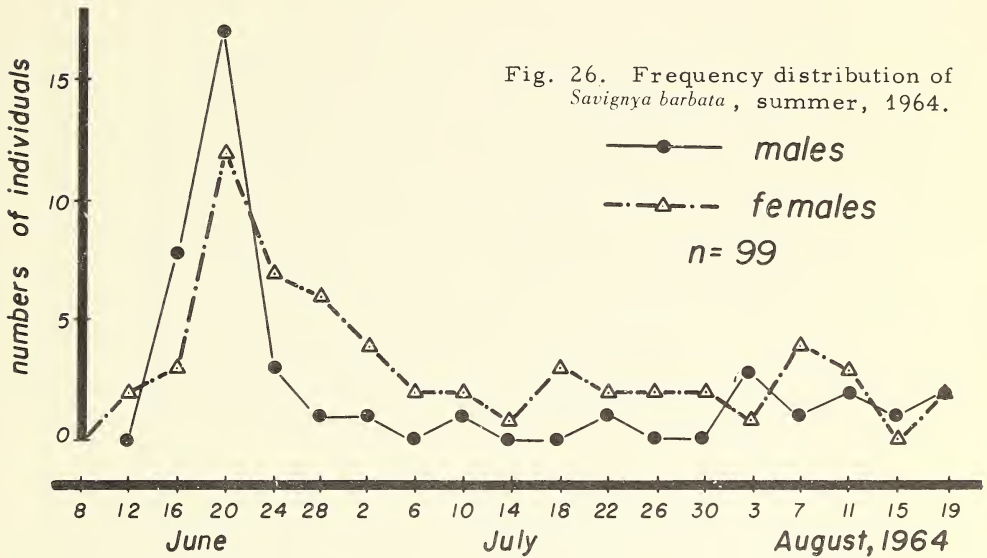


Fig. 27. Distribution of *Savignya barbata*.



*Description - Female.* Color: carapace brown, marked and shaded with dark brown; chelicerae brown; sternum brown; labium brown, but marked with gray; coxae of pedipalpi brown, but gnathobases gray; legs pale brown-yellow, distal part of each leg segment brownish; opisthosoma brown-gray; spinnerets brown-gray.

Structure: size small, about 1.90 mm total length; carapace longer than wide, 0.64 mm long x 0.54 mm wide, carapace broad and rounded, gradually rising to the low cephalic region; clypeus height about five diameters of an anterior median eye; posterior row of eyes slightly procurved; posterior medians about 1.5 diameters of one apart, and closer to the posterior laterals than to each other; anterior row of eyes slightly procurved; anterior medians less than the diameter of one apart, and about the diameter of one from the laterals; anterior laterals almost twice the size of an anterior median; median ocular quadrangle about as wide at posterior medians as long; chelicerae decidedly reclined; sternum about as wide as long; legs moderately long; metatarsus IV about 1.45 times longer than tarsus IV; tibia I-III with two spines, tibia IV with one spine at 0.29; Tm I about 0.63; Tm II about 0.54; Tm III about 0.48; Tm IV lacking.

Male. The male is colored like the female. Structure: size small, about 1.45 mm; carapace longer than wide, about 0.64 mm long x 0.54 mm wide; carapace structure like that of the female, except for a small, post-ocular sulcus and lobe that is finely-bridged and connecting behind each posterior median eye (see figures 55, 56); metatarsus IV about 1.29 times longer than tarsus IV; tibia I-III with two spines, tibia IV with one spine; Tm I about 0.56; Tm II about 0.53; Tm III about 0.50; Tm IV lacking. For the characteristic details of the pedipalp of the male, see figure 54.

*Natural history -* This species is a member of the humid arctic faunal element. The species is widely distributed throughout soggy, vegetated areas at and near pond edges, but is restricted to the night shadow areas. Individuals have been collected under water in slush snow at the time of the spring melt, and on wet, south-facing slopes and depressions abounding with sedges or mosses.

Figure 28 shows the abundance pattern of the species during the summer of 1964. It is not known if the adults overwinter, but it can be assumed that they do as the adults are found so early in the season.

*Material examined -* About 100 adult individuals of this species were examined from Hazen Camp and four males and two females from Axel-Heiberg Island (Heinz Rutz, collector, 1963). The holotype was not seen.

*Distribution* (fig. 29) - This species is known from three localities only, two on Ellesmere Island at Hazen Camp and either Rice Strait (78° 34'N, 74°45'W) or Fort Juliana (79°03'N, 77°43'W), and Axel-Heiberg Island.

*Xysticus deichmanni* Soerensen, 1898 p.228 (Figs. 40, 41)

*X. labradorensis*: Bonnet 1959 p.4883 (in part); *X. deichmanni*: Holm

1958b p. 533, Buckle and Redner 1964 p. 1139, Oliver 1963 p. 176, Turnbull, Dondale, and Redner 1965 p. 1263.

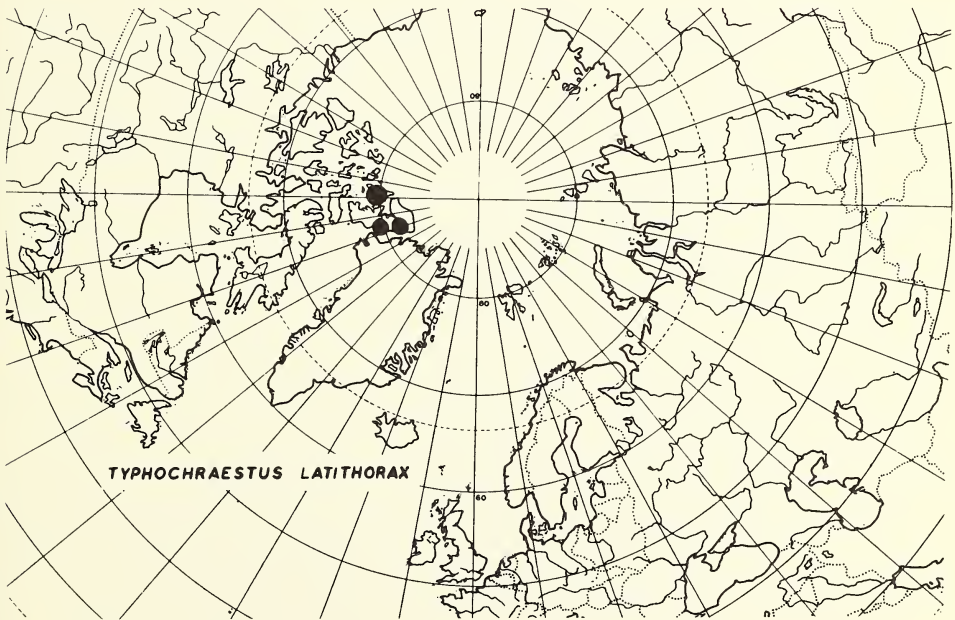
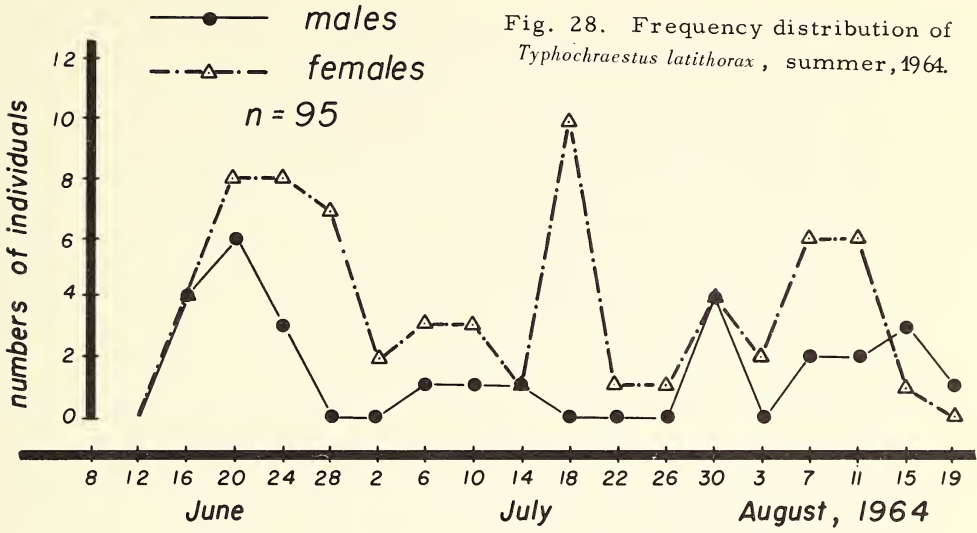


Fig. 29. Distribution of *Typhochraestus latithorax*.

*Notes on taxonomy* - Holm (1958b) and Buckle and Redner (1964) have distinguished the species *labradorensis* from *deichmanni*. The distribution records of the two species do not overlap.

*Natural history* - This species is a member of the arid arctic faunal element. Individuals at Hazen Camp were found with *Dictyna borealis* under and around *Dryas integrifolia*. The main difference observed about the habitat of the two species is that *X. deichmanni* remains mostly on the ground under and beside vegetation (occasionally in the *Dryas* flowers), whereas *D. borealis* is mostly on and in the vegetation. *X. deichmanni* was found mainly under and near *Dryas integrifolia* clumps, but occasionally near *Salix arctica* and *Kobresia myosuroides*.

Figure 30 shows the occurrence of the adults of this species during the summer of 1964. Data from 1963 are almost identical. The adults are able to overwinter, as is indicated by the late season increase.

The Thomisidae have little or no courtship preceding mating (Kaston 1936), and *Xysticus deichmanni* is no exception. In all four cases observed, the males mounted the females after a short contact or mounted directly upon contact without any hesitation. The females offered no resistance to any of the males. Once upon the females, the males tied down the females with silk. Silk threads were attached from the carapace to the patellae to the ground and back again many times. Once the female was thoroughly tied down, the male began to mate.

Before the actual mating, the male appeared to clean and polish the palpi in the chelicerae. Each palpus was very carefully rubbed and manipulated. When this was done, the male crawled back along the female, then around and under the posterior end of the opisthosoma of the female, then mated by alternately placing the palpi upon the epigynum. When mating, the pair are positioned venter to venter and facing the same direction (see Kaston 1936). The duration of the matings were 5, 52, 55.5 and 59 min each. In the case lasting five min, the male was successful in placing each embolus within the epigynum once before leaving the female. In the remaining cases, each palpus was placed on the epigynum for an average of about 14 min. The haematodocha was refilled and embolus re-inserted once every 20 sec. When the haematodocha refilled, the large dorsal and some smaller lateral spines on the legs of the male became erect for about two sec, then gradually over the next three sec, relaxed.

When the male was finished mating, he again crawled onto the dorsum of the female, polished the palpi in the chelicerae, paused, then fled rapidly. The males died about four days later.

As of October 8, 1964, no eggs were laid. Thus it can be assumed that the fertilized females overwinter and lay eggs in the following summer. Gertsch (1964, pers. comm.) has confirmed this. Sometime between October 8 and 18, 1964, eggs were laid in a small sac on the flat edge of a rock. There were 28 eggs. The sac was lenticular, about six mm in diameter, and about two mm in thickness in the centre.

The main food for the species seems to be small Diptera, especially Chironomidae and Culicidae. Oliver (1963, pers. comm.) found several instances where this species was feeding on the first instar larvae of

*Gynaephora rossi* Curtis and *G. groenlandica* (Hom.) (Lymantriidae, Lepidoptera) as they emerged from the eggs on the cocoon of the female. The first instar larvae are only about one mm long, and present no difficulty in grasping for the spider. Oliver (pers. comm.) and I have also found specimens hiding in *Dryas* flowers, presumably to catch visiting insects.

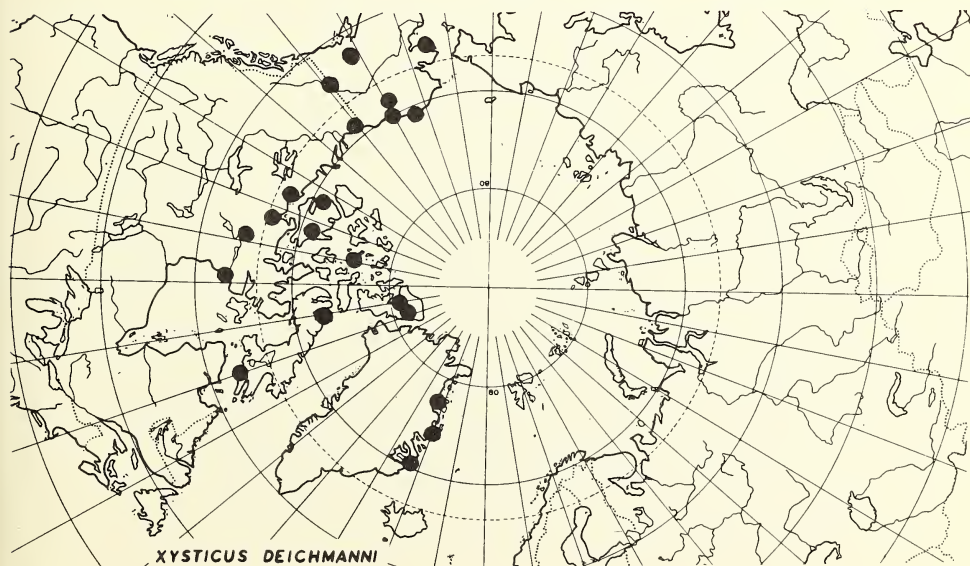
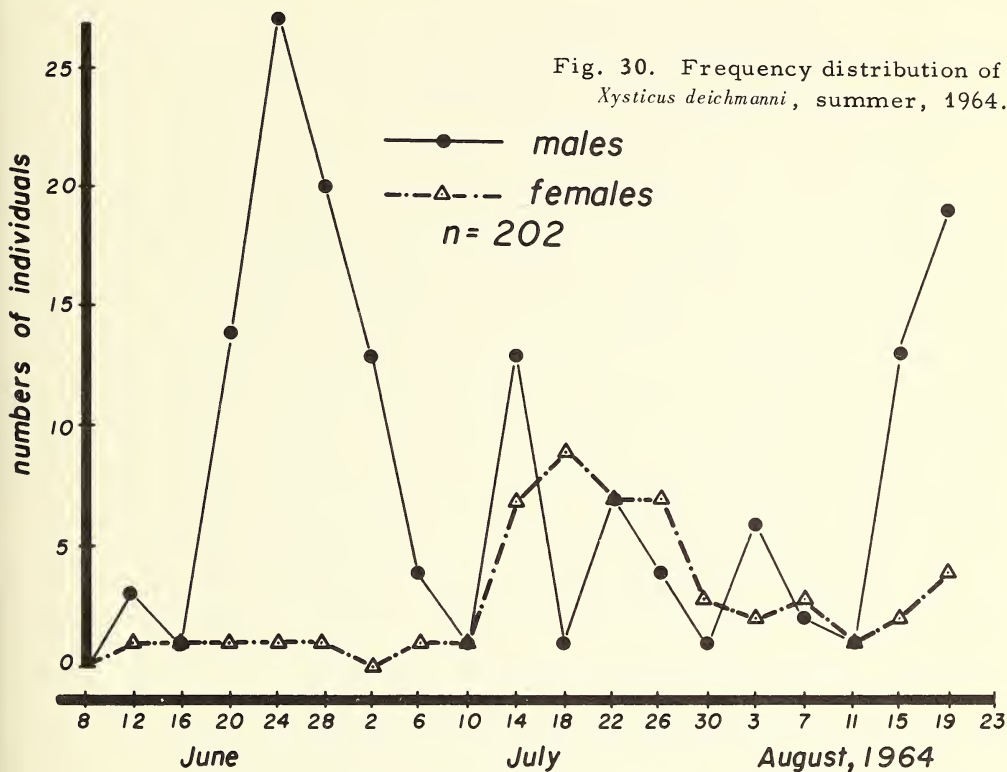


Fig. 31. Distribution map of *Xysticus deichmanni*.



In 1963, one female was found with a parasite, *Hexameris* species (Nematoda, Mermithidae), inside the opisthosoma. The epigynum was abnormal, indicating parasitic castration within.

The contents of the crop and gizzard of two snow buntings showed remains of legs and carapaces of *X. deichmanni*. There were also many observed cases of cannibalism.

*Material examined* - About 575 adults of this species were examined from Hazen Camp, and one male and one female from Chesterfield Inlet, N. W. T., and two females from Tanquary Fjord, Ellesmere Island (Guy Brassard, collector, 1964).

*Distribution* (fig. 31) - Greenland (N. E. Greenland between 70-78°N). Canada (Franklin District: near Ukpilik Lake, King's Bay, and Holman Island, Victoria Island; Hazen Camp and Tanquary Fjord, Ellesmere Island; Moose Bay, Bathurst Island; Lake Harbour, Baffin Island; mouth of the Aktinek River, Bylot Island, 70°N, 78°W; Keewatin District; N. W. side Aberdeen Lake; Chesterfield Inlet; Mackenzie District: Bathurst Inlet; Coppermine; Bernard Harbour; Yukon Territory: Firth River, 16 miles from the Arctic coast; Swede Dome, 34 miles W. Dawson City). Alaska (Mile 206, Richardson Highway; Nome; Point Barrow; Umiat; Meade River; and Cooper Landing).

Notes: Buckle and Redner (1964, p. 1141) record the Richardson Highway as being in the Yukon. This locality is really in Alaska, 206 miles north of Anchorage. The Holman Island locality referred to by these authors is most likely the townsite of Holman Island on Victoria Island, not the very small island off shore near the town. King's Bay, Victoria Island, for all intents and purposes, is the same locality as Holman Island.

## ZOOGEOGRAPHICAL CONSIDERATIONS

In 1934, Gelting, after an analysis of the botanical and geological evidence, proposed that the northeastern tip of Peary Land was ice free during the maxima of the ice ages, and that some other areas on Greenland were ice free during at least the Wisconsin Glaciation. The idea of ice free areas or "refugia" in Greenland was not his though, as Kornerup (1878) proposed this after a geological study, and Warming (1888) again, after a botanical study. Heated controversy for and against the theory of glacial refugia has occurred since then and the subject is still being debated (Ball 1963, Lindroth 1963a, Benson 1958, Nordhagen 1963).

In 1937, Eric Hultén published a monumental work on phytogeography in the arctic and boreal regions based on the premise of glacial refugia. Since then, most biologists agree that ice-bound refugia existed during glacial times (Savile 1961; Packer 1962, various authors in Löve and Löve 1963, various authors in Lowther 1959, 1962, Lindroth 1957, 1961, 1963a, 1963b, Larsson 1959, Harington 1964, Hammer 1955, Böcher *et al.* 1957, Ball 1963, McPhail 1961).

The basic premise upon which biologists have based theories of

glacial refugia (other than on geological evidence) is a more or less limited distribution of a species or of many species. The locality or area of the distribution is also held as significant. The greater the number of species in an area that have not (yet) been found in other areas, the greater the possibility that the area was a refugium. But the number of known species from an area and the distribution of the species concerned is most often directly proportional to the thoroughness of collecting that has been done.

No area in Canada is as thoroughly collected as the Hazen Camp area. This fact alone would ordinarily bias distribution patterns beyond use for zoogeographic purposes unless some criterion other than taxonomy is used.

I am therefore introducing data from insects and spiders, based on morphology, vagility, and biology, and some geological evidence, to support a suggestion that the northern part of Ellesmere Island had ice free areas during the Wisconsin Glacial division (and perhaps more divisions within the Pleistocene epoch) that served as glacial refugia.

Studies at Hazen Camp have uncovered about 350 species of insects, arachnids and Collembola, including several new species of Homoptera (Richards 1963, 1964a, b), Diptera (Oliver 1963, and pers. comm.), Coleoptera (W. J. Brown, unpubl. and J. A. Downes 1964), Hymenoptera (W. R. M. Mason, pers. comm.), and Acarina (E. Lindquist, pers. comm.). Except for two species of Ichneumonidae that are over five mm long that are scarce, the bulk of the new material from Hazen Camp is small (less than four mm long) and of generally cryptic, unstudied and poorly collected groups.

There are about 75 species of flightless insects in the Hazen Camp area. Most of them are brachypterous and some are apterous. Flightlessness in insects is not a rapidly developed feature, especially in peripheral or marginal regions, where species cannot get the extra energy necessary for morphological experimenting, and where emphasis is on feeding and breeding. I therefore suggest that these flightless insects have been on northern Ellesmere Island for part, if not all, of the Pleistocene epoch. Gressitt (1964, p. 595), in contrary opinion, states that selection favouring loss of wings in insects, particularly Diptera on Campbell Is., (N. Z.), is probably proceeding at a rapid rate. At Hazen Camp, however, no apterous Diptera were found, so either Gressitt's theory is wrong or else the flightless condition develops in insects at different rates in different areas (my inference).

To date, there are 14 species of Collembola and about 80 species of Acarina known from the Hazen Camp area. However, I do not believe that these two groups can be used for refugium analysis as they have the ability to colonize readily in areas where no other arthropod can and they do so very rapidly; the method of this rapid dispersal may be by wind (Gressitt *et al.* 1963, and Gressitt and Collaborators 1964) and by individuals and/or eggs on clods of dirt on birds' feet. Thus there is no way of calculating when these two groups came into an area.

Several species of spiders have probably remained on northern Ellesmere Island during most or all of the Pleistocene epoch. *Tarentula exasperans* was never observed to have a drag line, a feature that might

be analogous to flightlessness in insects (H. W. Levi, pers. comm.), and *Pardosa glacialis* and *Nysticus deichmanni* have drag lines that are so weak that they would not support the weight of even a third instar, a feature that might be analogous to brachyptery in insects (my inference).

In contrast, several immatures of *Dictyna borealis* were observed ballooning in early July, 1964. Braendegaard (1937, 1938) has made similar observations in Greenland and elsewhere. The remaining species of spiders, all Linyphiidae, have strong drag lines, indicating possibly recent immigration to the Hazen Camp area.

It appears that there are two basic zoogeographical groups of spiders at Hazen Camp: one group of three species that has withstood the Wisconsin Glaciation and probably most or all of the Pleistocene epoch on northern Ellesmere Island, and a second group that may have moved into the area recently.

The second group, that is, the recent immigrants, appears to have had two sources, one from the arctic zone and the other from the boreal or low arctic zone. Two species of Linyphiidae, *Typhochraestus latithorax* and *Minyriolus pampia* are confined to the night shadow area, and are thus possibly not yet adapted to the arctic light conditions. These night shadow areas are sunny during the day, but shaded during the period that would be night in the temperate regions. The shadow regions are often cooler "at night" than the sunny regions, hence these two species appear to have a diurnal rhythm. On this basis I suggest that these two species are recent immigrants from the temperate or low arctic regions. The remaining species of Linyphiidae are not confined to the night shadow regions. They display full adaptation to the arctic conditions of light. Their general Holarctic distribution indicates this as well.

Taxonomic evidence that the northern end of Ellesmere Island may have been a refugium is based on an analysis of muskoxen skulls by Harington (1964). Gjaerevoll (1963) states that there was a refugium somewhere in the Queen Elizabeth Islands, though he gives neither reasons nor references.

The geological evidence of a refugium on Ellesmere Island is divided. Hattersley-Smith (1961) suggests that any ice that might have been on the plateau between Lake Hazen and Alert was protective rather than erosive, as it is unlikely that the soft silts and lignite would have been preserved in an area where they are in part covered by a piedmont glacier at the present time. On the other hand, widespread erratics have been found in this area, though the date of deposition is not known.

I do not believe that during the Ice Ages of the Pleistocene epoch conditions were ever as severe as most are led to believe. It is fully possible that the conditions were so poor for several years in succession that the ice and snow did not melt off the ground, but equally possible that one season in four or five, or even ten, with favourable conditions melted the ice and snow and permitted life and growth to continue. Thus, even though there were about one and one-half million years in the Pleistocene epoch (Ericson *et al.* 1964), the effective time available for arthropods to have been active may have been as little as three hundred thousand years. If the Pleistocene epoch is shortened to three hundred thousand years as some authors believe it should be, then these animals have had



even less time to evolve the flightless condition.

In summary, it appears that there is one fauna on northern Ellesmere Island that has been there since before the Wisconsin Glaciation and perhaps for the duration of the Pleistocene epoch, and another fauna that may have immigrated to northern Ellesmere Island in post-Wisconsin times.

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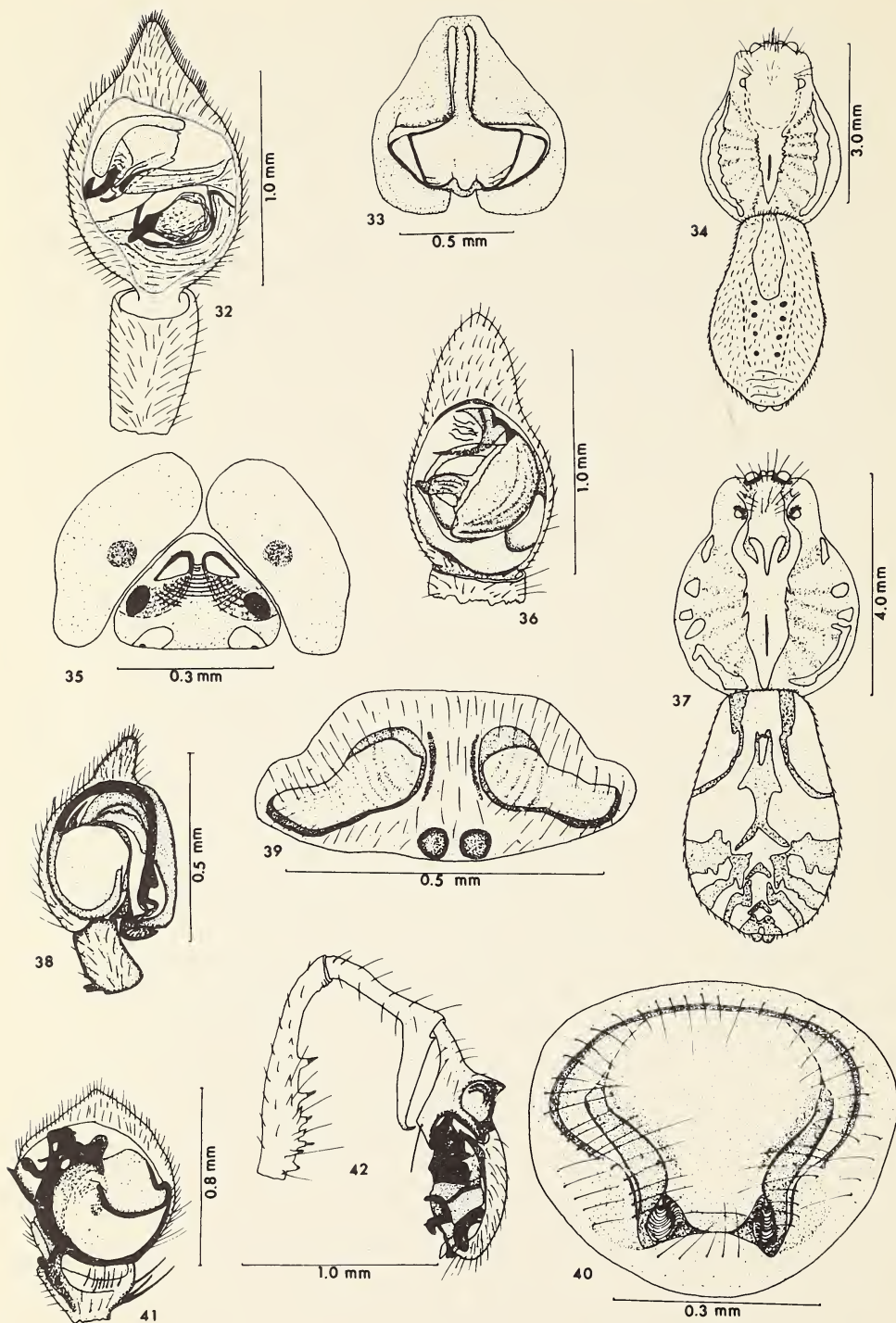
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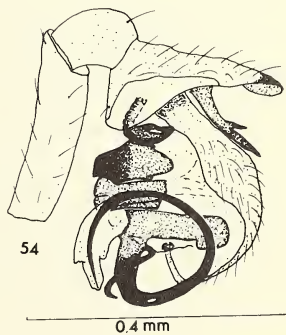
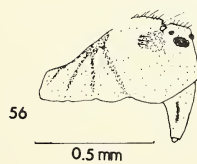
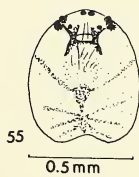
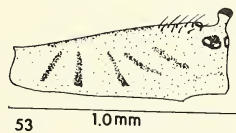
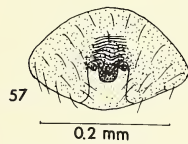
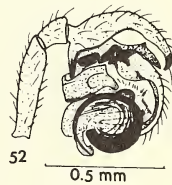
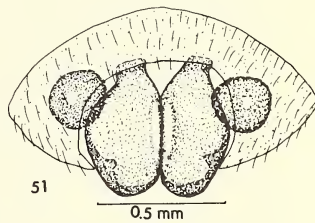
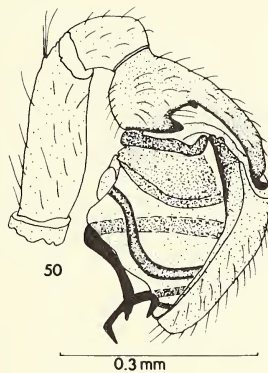
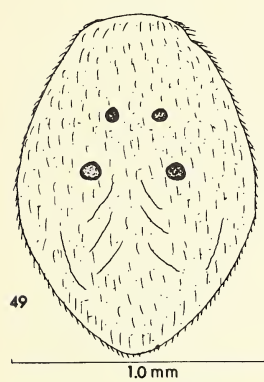
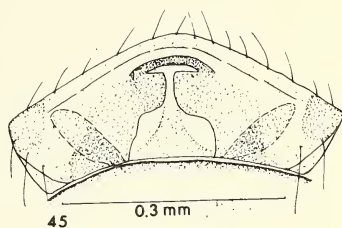
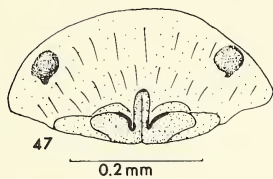
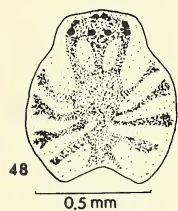
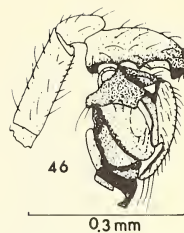
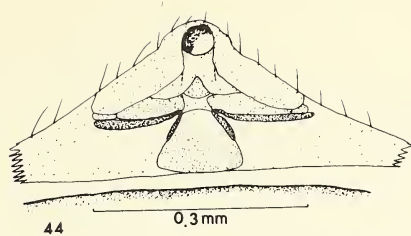
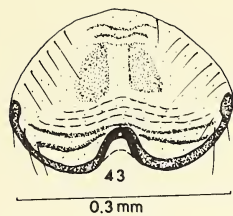
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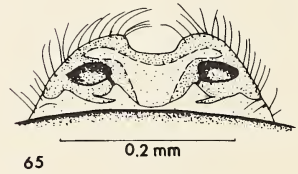
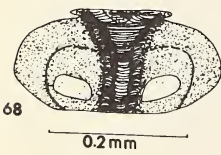
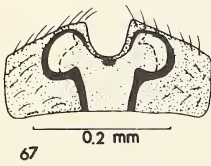
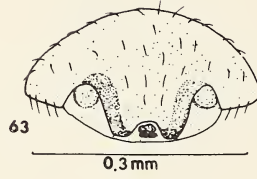
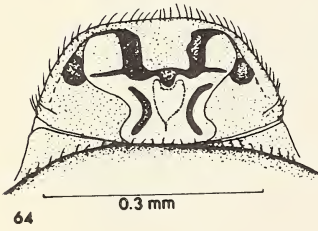
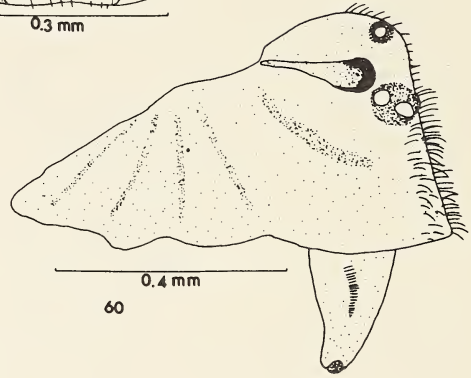
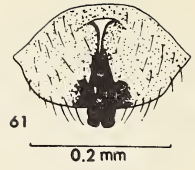
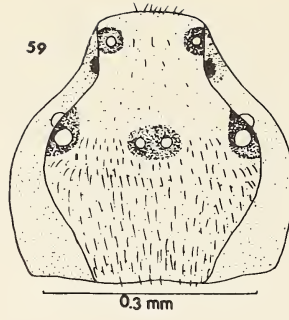
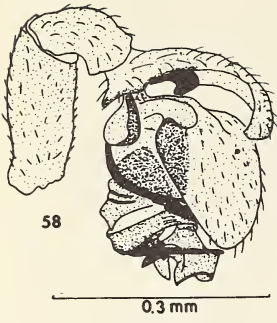
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### Book Review

ANNUAL REVIEW OF ENTOMOLOGY. Volume 11, 1966. Annual Reviews Incorporated, Palo Alto, California, in cooperation with the Entomological Society of America. viii + 596 pp. 3052 refs, 27 figs. \$8.50 U.S.A., \$9.00 elsewhere. With some comments on the first ten volumes.

This eleventh volume in the series is no less essential than any of its ten predecessors; in fact, perhaps the extra hundred or so pages over some of the earlier volumes make it more so. That it is essential, however, makes it particularly important that attention should be drawn to some of its shortcomings.

The title of a review article should, in a sense, be a review of its contents. Several titles here are not; the worst is the last review in the book, entitled "Pest Control", which covers little besides the control of industrial and domestic pests, an area last covered in Volume 1 of the Review. Jacobson's "Chemical insect attractants and repellents" ends abruptly after the heading Synthetic Repellents, an area of wide current interest, yet includes a treatment of phagostimulants - but only those in plants. The authors explain these things in part, but it would be better if they didn't have to.

The indexes to authors and subjects are invaluable. That to chapter titles could be much better organized; for years it has opened with the solecism ACARACIDES, while this is cross referenced to Insecticides, the only reference thereunder is spelt acaricides. More importantly, the main headings are not mutually exclusive: 'Application of Insecticides' and 'Resistance to Chemicals' should surely come under 'Insecticides and Toxicology'; 'Apiculture and Pollination' and 'Vectors of Plant Pathogens' should come under 'Agricultural Entomology', 'Population Ecology' under 'Ecology', and 'Nutrition' under 'Physiology'. While many chapter titles need duplicate entry under this system, only a few have been accorded this.

If the chapters of the first eleven volumes are tabulated under the following tentative system, they fall as indicated by the numbers in brackets, and very few titles present difficulties:-

Historical and General Entomology (1); Morphology (7); Taxonomy (20: general 12, apterygotes 0, exopterygotes 3, endopterygotes 5); Physiology (45); Ecology (47); Applied Entomology - General (45); Applied Entomology - Agricultural and Forest (25); Applied Entomology - Medical and Veterinary (22); Applied Entomology - Industrial and Domestic (2); Applied Entomology - Benefactory (9). This process reveals some imbalance in coverage, beyond that necessitated by the imbalance of the current research efforts of entomologists. Specifically, we could do with many more general articles (c.f. Remington and Remington, Volume 6); substantially more on morphology - including that revealed by electron microscopy; more taxonomy, especially of the apterygotes and exopterygotes; and more on industrial and domestic entomology - perhaps especially in the context of population ecology and new approaches to control. This same system suggested for indexing might well be used to impose some sequence on the chapters themselves; the random arrangement used hitherto, without even chapter numbers, has nothing to



recommend it to the user.

Several authors in Volume 11 find it necessary to apologise for this or that omission from their reviews, attributing this to space limitations. In so doing they squander space which might have been used to repair the omission. Most users of Annual Reviews know by now that space is limited.

Although "it is often (always?) easier to review our ignorance than to repair it" as Weaver says (page 79), we all owe an immense debt of gratitude to those who undertake the time-consuming task of writing these reviews. I particularly enjoyed Evans' delightful "Behaviour patterns of solitary wasps". Hoogstraal's "Ticks and human viral diseases" with 355 references is as complete and cosmopolitan a treatment as anybody could wish. The fine study of the Triatominae by Usinger and his allies, an original work as well as a review, is at the other end of the scale with 28 references. The 3052 references (less duplications) in the book as a whole comprise a substantial part of a year's accretion to the entomological literature. Other particularly timely and important contributions are Kroeger and Lezzi's "Gene action in insect development", Madelin's botanical approach in "Fungal parasites of insects", and perhaps the most hopeful sign for the future of applied entomology, Geier's "Management of insect pests".

The establishment of a special price for students is to be applauded.

Brian Hocking

#### CORRIGENDA

P. 8, para. 5, l. 6 delete "line", substitute: "reservoir and the genital opening, replacing the term ejaculatory duct".

P. 63, para 3, l. 6, delete "Odontotarsini", substitute "Odontoscelini".



Publication of *Questiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

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Volume 2

Number 3

4 July 1966

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## Editorial - Bridge builders?

It is a common weakness of peoples and generations brought up without history to attach undue importance to the discoveries of their own lifetimes. Amid the excitement over DNA and the endoplasmic reticulum and other revelations of the electron microscope and the ultracentrifuge, those of us who are aware we are aging may take comfort in the thought that an insect is still an insect and a plant still a plant and in the assurance that the solid body of knowledge handed down from previous generations, despite the thrilling rate at which it is being added to, remains essentially unassailable. Morphology remains morphology, though its horizon dips to the molecular level, into the limbo designated by that most unfortunate misnomer "ultrastructure".

Physiology remains physiology; it hasn't become biochemistry despite the cinderella status of biophysics and especially biomechanics; the new perspectives in this field do not alter its dependence on morphology. Indeed the revelations of molecular structure serve to emphasize more strongly than ever the necessity for a thorough understanding of structure before functional speculation or even experimentation is indulged in.

Those of us who are not yet aware that we are aging should be discomforted by the reflection that history and aging go hand in hand but that the one repeats itself and the other doesn't. It is, indeed, the repetitions of history which give it the perspective generating quality that makes it an essential part of the study of any subject.

Even a molecular biologist needs a name for a species he works with, and needs in consequence to be aware of the vagaries of names and their application and indeed of the principles of systematics. It makes no more sense at the molecular level than at any other to study the functions of an organ one cannot find, in a species one cannot name. And names, of course, have histories, even if we have decreed that those proceeding further back than 1758 should have academic status only, and

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these histories have a future. It might, in fact, be said that the purpose of most biological work, including that at the molecular level, is to contribute to the future of names. For evolution is no more than the history of life, and both has an end in itself and as a contribution to human welfare, nothing could be more central to biology than a detailed and accurate understanding of the past of evolution. This is the true aim of systematics; its attainment should permit predictions as to faunal future to replace the chaotic mayhem man occasions today. The provision of handles for taxa is but a serendipitous appendage.

Given this grand aim it is doubly unfortunate that biologists should attach to themselves such belittling prefixes as 'micro-' and 'molecular'. Surely better names can be found; perhaps it is even the bearing of these names that contributes to the very evident rift which has developed in recent years between micro-thinking groups in both the traditional and the molecular areas of biology, to the detriment of both. We cannot afford such little luxuries.

There is no better bridge between the macro and the micro than the entomologist; his subjects of study force him into both camps, they are both small enough and hardy enough to be superior subjects for micro and molecular study, and ubiquitous enough and diverse enough in structure, function, and relationships to compel attention from the traditionalist. People come to resemble the subjects of their studies; while we may describe the brains of insects as small, both relatively and absolutely, let us as entomologists stretch ours to build this bridge.

Brian Hocking

#### CORRIGENDA

P. 209 (Vol. II No. 2). For: Figs. 65-66, read Figs. 65 & 69.  
(*C. spetsbergensis*)

For: Figs. 67-69, read: Figs. 66-68.  
(*C. thulensis*)

## THE ARRIVAL PATTERN OF TRICHOPTERA AT ARTIFICIAL LIGHT NEAR MONTREAL, QUEBEC \*

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*Quaestiones entomologicae*  
2 : 217 - 242 1966

*The arrival pattern of Trichoptera at artificial light at Ile Ste. Hélène, in the St. Lawrence River opposite Montreal, Quebec, is examined. A Robinson trap with a mercury vapour light bulb was combined with a Lafrance trap which changed containers hourly. Ten minute catch periods were used to examine the evening peak in detail, containers being changed manually. Numbers and sex ratios for each of 78 species taken are given. One species not then described, and two other doubtful forms, females, were noted. Thirty one genera and thirteen families are represented. The pattern in each of 7 species examined in detail is nocturnally bimodal, with only a small morning peak. The roles of light, temperature, wind, relative humidity, and saturation deficit in determining total catches per night and fluctuations of numbers within any one night, are examined. Temperature and wind are the primary factors, with light fixing the time of the evening and morning peaks. Neither relative humidity nor saturation deficit seemed to be of any significance, at the values experienced. A differential effect of wind on flight, depending on species size, is shown. Sex ratios throughout the night are briefly examined, and it is concluded that no one sex of any of the seven major species is alone responsible for any peak. It is considered that the pattern of arrival at light reflects a natural pattern of flight activity.*

It has previously been found that in East Africa (Corbet & Tjønnealand 1955) the numbers of Trichoptera at lights vary throughout the night according to a pattern. This study is an investigation of the arrival pattern of Trichoptera at artificial light at night at Ile Ste. Hélène in the St. Lawrence River opposite Montreal, Quebec. The effects of meteorological factors, including natural light, on the pattern were examined. While the study deals with the pattern of arrival at artificial light, and the results can only be directly interpreted within the observed conditions, some attempt is made in the discussion to relate the pattern found to the natural pattern of flight activity, independent of artificial stimuli.

### METHODS AND EQUIPMENT

To examine patterns of animal activity relative to time, the time involved must be subdivided to a number of equal periods, here called 'catch periods' or just 'periods'. The population at light was sampled during successive catch periods. To compare patterns between nights and obtain meaningful average patterns for the summer, it is necessary to start any one chosen catch period at the same solar time each evening.

\* Publication No. 6 resulting from the World Exhibition Shadfly Project: Canada Department of Agriculture, Research Branch; Provincial Department of Agriculture, Quebec; and Canadian Corporation for the 1967 World Exhibition.



Two solar times were used: sunset (solar elevation minus  $0.83^\circ$ ) and civil twilight (solar elevation minus  $6^\circ$ ). These times, translated to local clock time for each night, were obtained from tables prepared by the Dominion Observatory, Ottawa, and the Meteorology Branch of the Canada Department of Agriculture, Ottawa. The times were prepared for the latitude and longitude of Ile Ste. H  l  ne ( $45^\circ 31'N$ ,  $73^\circ 32'W$ ).

It was decided to examine the pattern of the entire night using 1 hr catch periods, the first of which was to start one half hour prior to sunset, and to examine the evening peak in more detail, using 10 minute periods, starting one hour prior to civil twilight. Civil twilight was used for the 10 min catches as it was noted after running several nights at 1 hr periods that the massive upsurge to the evening peak generally occurred in the second period, in which civil twilight also occurred. It was felt that civil twilight might be of significance to the evening peak of flight activity and the 10 min sessions were designed to determine the timing and form of the evening peak, and perhaps the factors controlling it.

The 1 hr catching period nights always ran for a total of 12 hrs as this was the capacity of the automatic trap used and covered the entire night, ending well past sunrise. As many as 19 ten minute periods were run on some nights, but 13 was decided on as the minimum which sufficed to cover the period of peak flight activity. On one night trapping was stopped after 9 periods due to cold; the data are only used in the results when considering catch nights individually.

#### Trapping Methods and Equipment

Trapping was done at the old Fort (figs. 1 & 2). The 1 hr catches were taken with a mechanical trapping device designed and built by Mr. J. Lafrance (1965) of the Canada Department of Agriculture Laboratory, St. Jean, Quebec, and loaned for this study. It is capable of hourly ( $\pm 2$  min) changing of catch canisters, but can be adjusted for other periods. Capacity is 12 canisters, and the killing agent used was 70% ethanol.

The insects reached the cans by way of a large funnel on top of the trap body, with the spout passing through the roof to the cans below. On top of the funnel was placed the metal cone of a Robinson trap (Robinson & Robinson 1950), which bears a socket for an 'Osram' 125 watt, high pressure mercury vapour light bulb (230-240 volts; model MB/V). The light from this bulb is particularly rich in UV light, and is highly attractive to Trichoptera in consequence (Williams 1954). The spectral composition of light from a similar source is given in table 1. A cylindrical collar, 7" high by 13" diameter, made of file-folder card was placed around the upper edge of the Robinson cone to reduce the intensity after an abortive first use of the trap in which so many Trichoptera arrived as to swamp the cans and necessitate rejection of the catches for that night. It was used for both 1 hr and 10 min catches. Even so, some of the catches taken on some nights were beyond the capacity of the machine. When this was so the entire night's catches were discarded. Intrinsic to the Robinson trap cone are 4 vanes set at  $90^\circ$  to each other on the inner surface, which serve to stun the insects as they spiral inwards and downwards towards the light; they then fall into the ethanol below. The vanes also served to hold the collar in place and hold the light bulb socket. This part of the Robinson trap was retained and temporarily coupled to the Lafrance trap.

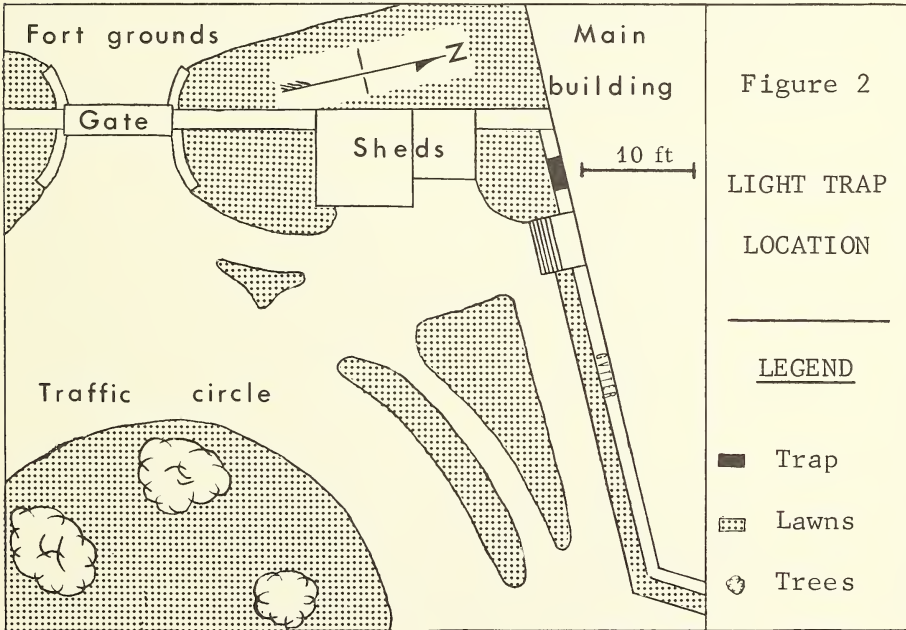
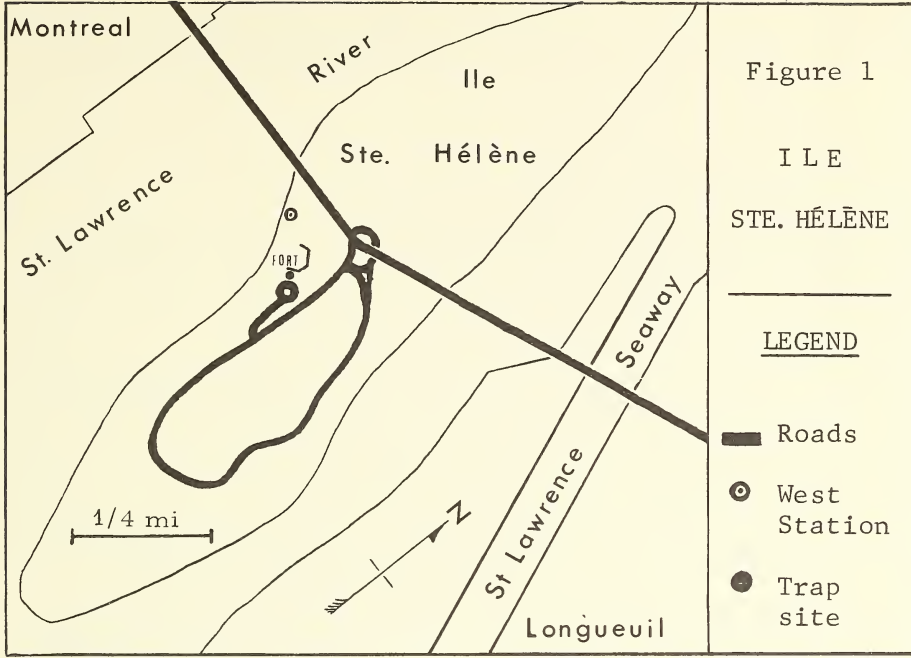


TABLE 1 - Intensity of the radiation from a high pressure mercury vapour bulb corrected for transmission through lime - soda glass (from Rössler 1939).

Wavelength (Å)	5791	5770	5461	4916	4358	4047*	3906
		-5791					
Relative energy in watts	6.39	4.99	6.10	.063	4.90	3.23	.054
Wavelength (Å)	3650	3341	3126	3022	2967	2925	2894
Relative energy in watts	6.62	.374	1.51	.215	.046	.002	.004

\* Lower limit of visible radiation in this spectrum.

The same equipment was used to take the 10 minute catches except that as the Lafrance trap could not be set for ten minute intervals, the jar was changed manually every ten minutes. Other conditions were as identical as possible to those of the 1 hr catch periods. The nights on which trapping took place, and other relevant data, are set out in table 2 (1 hr catches) and table 3 (10 min catches).

TABLE 2 - Dates and times (eastern daylight saving) of the first of 12 consecutive 1 hr catches of Trichoptera at Ile Ste. Hélène Montreal, summer 1964.

Date	Correct sunset time	Start of first period (p.m.)	Error (mins)
13-14 June	8.45	8.15	0
16-17 "	8.45	8.15	0
17-18 "	8.45	8.15	0
27-28 "	8.48	8.18	0
1 - 2 July	8.47	8.17	0
4 - 5 "	8.46	8.16	0
6 - 7 "	8.45	8.16	+1
13-14 "	8.41	8.12	+1
18-19 "	8.38	8.09	+1
23-24 "	8.33	8.04	+1
1 - 2 August	8.22	7.54	+2
3 - 4 "	8.19	7.52	+3
8 - 9 "	8.13	7.45	+2
12-13 "	8.06	7.39	+3
19-20 " *	7.55	7.25	0
25-26 "	7.44	7.14	0

\* Catch 12 not obtained.

TABLE 3 - Dates and times (eastern daylight saving) of the first of series of 10 minute catches of Trichoptera, at Ile Ste. Hélène, Montreal, summer 1964.

Date	Start (p. m.)* of first catch	Number of catches	End of last catch
2 - 3 July	8.24	19	11.34
7 - 8 "	8.23	16	11.03
14-15 "	8.18	18	11.18
19-20 "	8.14	14	10.34
24-25 "	8.09	18	11.09
6 - 7 August	7.51	13	10.01
13-14 "	7.50	9	9.20
23-24 "	7.22	13	9.23
26-27 "	7.17	13	9.27
30-31 "	7.09	13	9.19

\* One hour prior to civil twilight.

#### Other Observations

All the 1 hr catches were taken in the period for which continuous records of temperature, relative humidity, wind, and rainfall were made on the island, except that wind recording started after the first trapping night, June 13. The records used here are from the West Station (see fig. 1), about 20 ft horizontally from the edge of the river, but about 50 ft above the water and 1/4 mile from the trapping site. The station was setup and maintained by the Canada Department of Transport, in conjunction with the Shadfly Project.

Temperature and relative humidity were read from the charts obtained at the mid-point of each 1 hr catch period; wind speed, in miles per hour, is averaged for each catch period; saturation deficit was obtained from temperature and relative humidity by tables. Zenith light intensity readings were taken at the mid-point of each 10 min period. It was later discovered that the light readings could not be converted to foot-candles as the precise spectral sensitivity of the sensor unit was unknown and could not easily be determined. It has been possible, however, to obtain a curve of light intensity in arbitrary units (p. 238). As time permitted, notes on cloud, rainfall, and wind were taken.

#### Treatment of Catches and Data

Generally, all Trichoptera taken were determined to species and sex. Without exception all were counted. But occasionally a species or group of species, Hydroptilidae especially but also Hydropsychidae and *Protoptila maculata* (Hagen), were taken in such numbers that the proportions of each species and sex had to be estimated from a sub-sample. Selection of sample size was arbitrary but in general the larger the total numbers, the smaller the per cent sampled.



To reduce the effect of fluctuations due to environmental factors, the arithmetic values ( $n$ ) may be transformed to the logarithmic value ( $\log n$ ). To bypass the difficulty of zeros, for which there is no logarithmic value, Williams (1937) suggested adding one (1) to all values in a time series, and transforming the resulting values ( $n + 1$ ) to logarithms. If the  $\log (n + 1)$  values for all periods of any one time series, or equivalent periods in terms of solar time of several time series are averaged,  $[\sum \log (n + 1)] / N$  and the antilog taken, an approximation to the geometric mean of the series is obtained. This approximation is known as Williams' mean (Haddow 1960), and is symbolized as  $M_w$ . The value  $\sum \log (n + 1) / N$ , when obtained for equivalent periods of several time series and plotted against time gives an average pattern for these time series.

## RESULTS

### Numbers of Specimens Examined

Table 4 lists the species taken, in descending order of numbers taken per species in all catches. The total number of specimens of Trichoptera was 297, 967 for all species. A total of 78 species, in 31 genera and 13 families was taken, plus 2 doubtful forms. One of these, *Cheumatopsyche montrealensis* Nimmo (1966) was not then described. The following species were selected for detailed examination of data, and are given in order of abundance: *Hydroptila spatulata* Morton, *Cheumatopsyche speciosa* (Banks), *Protophila maculata* (Hagen), *Hydropsyche recurvata* Banks, *Psychomyia flavida* Hagen, *Athripsodes cancellatus* (Betten), and *Athripsodes tarsipunctatus* (Vorhies). *Agraylea multipunctata* Curtis was not selected although more numerous than *Athripsodes tarsipunctatus* because the catch was spread over 27 nights whereas that of *A. tarsipunctatus* was concentrated into 18. Also in table 4, the total numbers per species are broken down to sexes, sex ratios (per cent males) as in Henderson, Henderson & Kenneth (1960), and finally the range of dates on which each species was taken is given, concerning which it must be remembered that trapping started on June 2 and ended August 31.

The ratios may be artifacts of the trapping method, due to differential attraction of the sexes. One remarkable fact emerges from table 4, however. *P. flavida* shows a sex ratio of virtually zero. Marshall (1939) obtained similar results, but cautioned about the possible differential attraction. Betten (1934) states that he had only 2 specimens, females, but that Sibley (1926) took 893, in an unspecified manner, all of them female. If this is the natural ratio, then *P. flavida* must be usually parthenogenetic. Crichton (1960) considers in detail only the ratios of species with over 100 individuals taken, which is also done here. Only 26 species qualify of which 17 give ratios above 50, 3 of them close to this: *Leptocella candida* (52.00), *Agraylea multipunctata* (53.05) and *Athripsodes ancylus* (53.78).

### Pattern of Arrival at Artificial Light

The data will be examined first in the form of total numbers of Trichoptera per catch, after which the separate data on the previously selected species will be examined, for both 1 hr and 10 min catches.

TABLE 4 - Species of Trichoptera taken at Ile Ste. Hélène, Montreal, summer 1964 in descending order of numbers taken in both 1 hr and 10 min catches.

Species	Total	♂	Sex ratio (%♂)	Range of dates when taken
<i>Hydroptila spatulata</i> Morton	114,980	94,220	81.94	13 Jun. -30 Aug.
<i>Cheumatopsyche speciosa</i> (Banks)	54,582	25,616	46.93	13 Jun. -30 Aug.
<i>Protophila maculata</i> (Hagen)	50,738	30,323	59.76	19 Jun. -30 Aug.
<i>Hydropsyche recurvata</i> Banks	32,515	18,190	56.82	2 Jun. -30 Aug.
<i>Psychomyia flavida</i> Hagen	13,015	2	0.02	13 Jun. -30 Aug.
<i>Athripsodes cancellatus</i> (Betten)	9,951	7,766	78.04	1 Jul. -26 Aug.
<i>Agraylea multipunctata</i> Curtis	5,229	2,773	53.05	3 Jun. -30 Aug.
<i>Athripsodes tarsipunctatus</i> (Vorh.)	4,107	2,985	72.68	27 Jun. -25 Aug.
<i>Cheumatopsyche campyla</i> Ross	2,598	716	27.56	2 Jun. -30 Aug.
<i>Hydroptila waskesia</i> Ross	1,598	1,466	91.74	1 Jul. -20 Aug.
<i>Hydroptila waubesiana</i> Betten	1,182	817	69.12	13 Jun. -30 Aug.
<i>Glossosoma lividum</i> (Hagen)	897	541	60.30	2 Jun. -30 Aug.
<i>Oecetis inconspicua</i> (Walker)	695	276	39.70	16 Jun. -30 Aug.
<i>Athripsodes annulicornis</i> (Steph.)	674	231	34.27	2 Jun. - 5 Jul.
<i>Cheumatopsyche sordida</i> (Hagen)	610	185	30.30	27 Jun. -30 Aug.
<i>Hydropsyche morosa</i> Hagen	600	498	83.00	2 Jul. -30 Aug.
<i>Hydropsyche scalaris</i> Hagen	593	294	49.60	4 Jul. -30 Aug.
<i>Hydroptila perdita</i> Morton	577	530	91.80	14 Jun. -30 Aug.
<i>Hydropsyche bifida</i> Banks	440	237	53.80	13 Jun. -25 Aug.
<i>Polycentropus cinereus</i> Hagen	428	311	72.60	14 Jun. -30 Aug.
<i>Neureclipsis crepuscularis</i> (Walker)	341	247	72.40	14 Jun. -30 Aug.
<i>Leptocella candida</i> (Hagen)	325	168	52.00	27 Jul. -30 Aug.
<i>Brachycentrus lateralis</i> (Say)	184	80	43.40	2 Jun. -14 Jun.
<i>Hydropsyche placoda</i> Ross	146	107	73.20	13 Jun. -26 Aug.
<i>Oecetis immobilis</i> (Hagen)	121	31	25.60	1 Jul. -30 Aug.
<i>Athripsodes ancylus</i> (Vorhies)	106	57	53.70	27 Jun. - 1 Aug.
<i>Chimarra socia</i> Hagen	96	59		19 Jun. -30 Aug.
<i>Macronemum zebratum</i> (Hagen)	92	59		27 Jun. - 1 Aug.
<i>Athripsodes angustus</i> (Banks)	63	23		14 Jul. - 8 Aug.
<i>Mystacides sepulchralis</i> (Walker)	59	36		27 Jun. -30 Aug.
<i>Helicopsyche borealis</i> (Hagen)	50	45		27 Jun. - 3 Aug.
<i>Nyctiophylax vestitus</i> (Hagen)	41	28		28 Jun. -19 Aug.
<i>Oecetis cinerascens</i> (Hagen)	41	24		2 Jul. -30 Aug.
<i>Leptocella albida</i> (Walker)	39	24		2 Jul. -25 Aug.
<i>Hydropsyche walkeri</i> Betten & Mosely	37	27		28 Jun. - 1 Aug.
<i>Hydropsyche bronta</i> Ross	19	12		19 Jun. -30 Aug.
<i>Athripsodes punctatus</i> (Banks)	19	8		13 Jul. - 1 Aug.
<i>Hydroptila albicomis</i> Hagen	17	16		13 Jul.; 6,30 Aug.
<i>Athripsodes resurgens</i> (Walker)	14	12		13 Jun. -19 Jul.
<i>Athripsodes submacula</i> (Walker)	14	10		13 Jun. -19 Jul.
<i>Triacnodes flavescens</i> Banks	14	1		13 Jul. -30 Aug.

TABLE 4 (cont.)

Species	Total	♂	Sex ratio (%♂)	Range of dates when taken
<i>Trienodes injusta</i> (Hagen)	12	3		1 Jul. - 7 Jul.
<i>Chimarra obscura</i> (Walker)	9	7		1 Jul. - 19 Jul.
<i>Oecetis avara</i> (Banks)	8	6		6 Jul. - 3 Aug.
<i>Leptocerus americanus</i> (Banks)	7	1		2 Jul. - 14 Jul.
<i>Athripsodes alagmus</i> Ross	6	6		1 & 3 Aug.
<i>Chematopsyche analis</i> (Banks)	6	2		27 Jun. & 1 Aug.
<i>Hydroptila hamata</i> Morton	6	4		2, 14 Jul., 6 Aug.
<i>Trienodes marginata</i> Sibley	6	3		27 Jun. - 30 Aug.
<i>Oecetis osteni</i> Milne	5	1		13 Jul., 26, 30 Aug.
<i>Athripsodes dilutus</i> (Hagen)	4	2		2 Jun. - 5 Jul.
<i>Limnephilus moestus</i> Banks	4	2		14 Jun. & 2 Jul.
<i>Molanna musetta</i> Betten	4	3		5 Jul.
<i>Neotrichia okopa</i> Ross	4	2		7 & 19 Jul.
<i>Athripsodes uvalo</i> Ross	3	2		24 Jul. & 25 Aug.
<i>Cheumatopsyche montrealensis</i> Nimmo	3	3		27 Jun.
<i>Molanna</i> sp.	3	0		2 & 13 Jul.
<i>Banksiola selina</i> Betten	2	0		14 Jun. & 2 Jul.
<i>Hydropsyche</i> sp.	2	0		13 Jun. & 8 Aug.
<i>Lepidostoma togatum</i> (Hagen)	2	0		17 Jun. & 2 Jul.
<i>Limnephilus ornatus</i> Banks	2	0		28 Jun. & 5 Jul.
<i>Limnephilus submonilifer</i> Walker	2	0		17, 28 Jun., 2 Jul.
<i>Neureclipsis validus</i> (Walker)	2	0		2 & 5 Jul.
<i>Phylocentropus placidus</i> (Banks)	2	0		7 Jul. & 12 Aug.
<i>Agapetus hessi</i> Leonard & Leonard	1	0		27 Jun.
<i>Anabolia ozburni</i> (Milne)	1	0		2 Jul.
<i>Cernotina</i> sp.	1	0		19 Jul.
<i>Hydropsyche vexe</i> Ross	1	0		14 Jun.
<i>Hydroptila armata</i> Ross	1	0		19 Jul.
<i>Hydroptila consimilis</i> Morton	1	0		6 Aug.
<i>Hydroptila virgata</i> Ross	1	0		7 Jul.
<i>Hydroptila</i> sp.	1	0		13 Jul.
<i>Leptocalla exquisita</i> (Walker)	1	0		19 Aug.
<i>Limnephilus hyalinus</i> Hagen	1	0		2 Jul.
<i>Neureclipsis bimaculatus</i> (L.)	1	0		7 Jul.
<i>Polycentropus nasotius</i> Ross	1	1		5 Jul.
<i>Rhyacophila melita</i> Ross	1	1		14 Jun.
<i>Setodes oligia</i> (Ross)	1	0		7 Jul.
<i>Trienodes dipsia</i> Ross	1	1		1 Jul.
<i>Trienodes tarda</i> Milne	1	0		3 Jul.

Grand total 297, 967

Species patterns follow closely the total numbers patterns. The average pattern for each species for the summer, will, however, be presented. Only 1 hr catches will be considered relative to weather, as it is impossible to read values accurately from the meteorological charts for intervals as small as 10 minutes.

*1 Hour Catches - Total Numbers per Catch*

In fig. 3 a peak occurs generally in the second period. In 2 of 15 nights the peak occurred in period three. This may be due to extrinsic factors obscuring or delaying the peak. A second peak, slight or otherwise, is found in the first or second period immediately prior to sunrise. This is the morning peak.

Between the two peaks, evening and morning, it is seen that adults are taken, occasionally in very nicely decreasing series, as in fig. 3 (25-26 August), but often in widely varying numbers.

The average pattern for the summer, as determined by the nights on which trapping was carried out, is shown by fig. 4 (total numbers). The distinct evening peak is seen, but the morning peak is not manifest. This is due to sunrise shift during the season in relation to sunset and hence also in relation to the catch periods.

It remains now to demonstrate the dependence of the peaks on natural light intensity, and to explain the intervening period of gradual decline, or fluctuation as the case may be.

*Dependence of the Peaks on Natural Light Intensity*

The least fluctuating nightly graphs are selected for visual examination of the concomitant environmental factors. These graphs of fig. 3 (17-18 June, 13-14 July, and 25-26 August) show the peaks well. Table 5 presents the meteorological data for these three nights and examination shows that temperature is either declining throughout the night, usually slowly, or holding steady, but never increasing. Next, wind holds steady for at least the first two periods, in which the evening peak occurs. Finally, relative humidity and saturation deficit seem to fluctuate erratically. On the night of 13-14 July, however, they held steady for 5 hours preceding and including the morning peak. This seems to rule out these two factors as influencing the peak, at least at the values encountered here.

Thus meteorological factors are either declining fairly evenly, holding steady, or fluctuating and showing no correlation with  $\log(n+1)$ , yet the peaks occur outstandingly. The first catch is fixed on time of sunset, and the evening peak always occurs in the same period, the second. The morning peak may occur in period 9, 10, or 11, depending on the season, but always in the pre-sunrise period.

Table 5 omits only light intensity. In the evening, with all factors generally declining, there is a peak in numbers of Trichoptera caught. In the morning, the same conditions prevailing, there is another peak in numbers caught. The only factor which has equal values in both evening and morning is light intensity. Obviously from the graphs, the light values involved occur after sunset and before sunrise. Thus the causal (or triggering) factor of both peaks appears to be a certain light intensity.



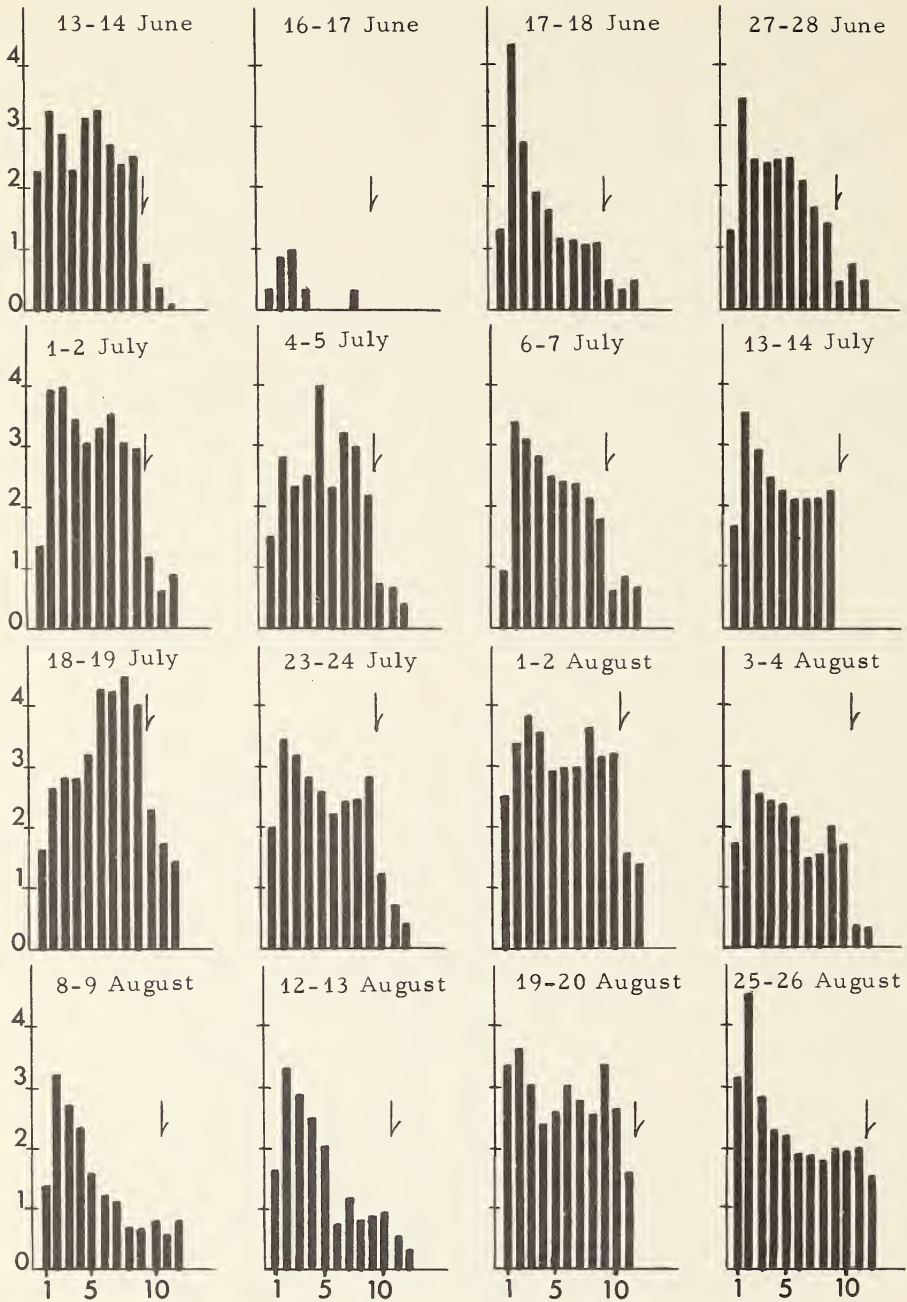


Figure 3 - Total hourly numbers of Trichoptera at UV light, Ile Ste. Hélène, Montreal, summer 1964. Abscissae 1 hr periods, ordinates  $\log(n+1)$ , plotted at the period mid-points: Sunset coincident with first period mid-point. Arrows indicate approximate sunrise.

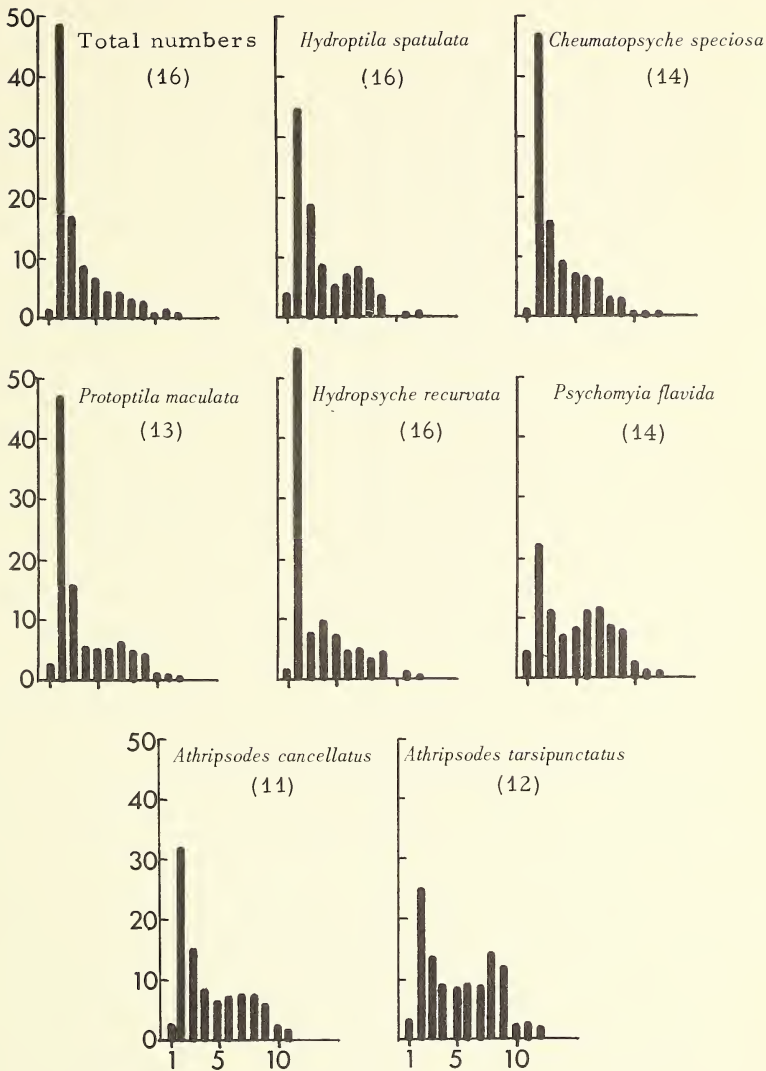


Figure 4 - Total numbers and numbers of 7 species of Trichoptera separately, taken at Ile Ste. Hélène, Montreal, in a UV light trap on 16 nights (or fewer), 1964; average values per 1 hr period for the summer. Abscissae 1 hr periods, ordinates Williams' mean ( $M_w$ ) transformed to %. Sunset coincident with the first period mid-point.

TABLE 5 - Meteorological data and log (n + 1) of total numbers of Trichoptera taken per 1 hr period at Ile Ste. Hélène, Montreal, on three selected evenings, summer 1964.

June 17-18	Per- iod	log (n + 1)	T°F	Wind mph	% R. H.	* S. D.
	1	1.30	63.5	6	29	0.42
	2	4.40**	63.0	7	32	0.39
	3	2.79	62.0	7	36	0.36
	4	1.89	61.0	7	39	0.33
	5	1.65	60.0	9	42	0.30
	6	1.18	60.0	8	46	0.28
	7	1.14	60.0	8	47	0.27
	8	1.04	59.0	10	49	0.25
	9	1.11**	60.0	9	50	0.26
	10	0.48	63.0	6	53	0.27
	11	0.30	63.0	7	57	0.25
July 13-14						
	1	1.62	71.0	2	85	0.11
	2	3.51**	70.0	1	82	0.12
	3	2.89	69.5	3	81	0.14
	4	2.42	69.5	3	84	0.12
	5	2.25	69.0	2	89	0.08
	6	2.09	68.5	2	88	0.08
	7	2.09	68.0	2	88	0.08
	8	2.08	68.0	2	88	0.08
	9	2.21**	68.0	1	88	0.08
	10	0	68.5	2	86	0.09
	11	0	69.0	1	84	0.10
August 25-26						
	1	3.14	73.0	9	58	0.34
	2	4.45**	69.0	9	60	0.28
	3	2.76	67.0	19	54	0.30
	4	2.21	67.0	19	70	0.20
	5	2.15	67.0	18	76	0.16
	6	1.81	67.0	15	79	0.14
	7	1.77	67.0	14	79	0.14
	8	1.74	66.0	15	76	0.15
	9	1.91	65.0	14	71	0.18
	10	1.85	64.0	14	72	0.17
	11	1.98**	63.0	13	72	0.17

\* S.D. = saturation deficit, in inches of mercury.

\*\* Peaks.

*Effects of Other Environmental Factors*

*The night as a whole* - Examined here are those periods of each night between and including sunset and sunrise.

Means of each factor, temperature, wind speed, relative humidity, and saturation deficit were obtained for each night. Each factor was then plotted against the mean  $\log (n + 1)$  values for each night. As seen in fig. 5, temperature and  $\log (n + 1)$  are clearly correlated; no other factor showed any significant correlation. That is, on an evening of high temperatures (70-80°F) one can expect a large catch, the opposite also holding true. Correlation coefficients are not calculated here as this is preliminary to an analysis of the data for the periods without sunlight. It should be noted that catches may be low despite high temperatures, due to relative seasonal scarcity of Trichoptera. This explains some lack of correlation in fig. 5. Other unrecorded or unrecognized factors may also be involved. Wind speed shows little apparent correlation with  $\log (n + 1)$ , although it can have a distinct effect on flight activity. The best available example is the night of 18-19 July (table 6):

TABLE 6 - Total numbers of Trichoptera taken, and meteorological data for 1 hr catch periods 1-9, 18-19 July, Ile Ste. Hélène, Montreal.

Catch period -	1	2	3	4	5	6	7	8	9
Log (n + 1)	1.60	2.57	2.73	2.71	3.15	4.20	4.15	4.40	3.91
T°F	89	88	87	86	85	85	84	83	83
Wind speed (mph)	24	25	25	23	14	8	5	3	1

Temperature was high and decreasing slowly. While a morning peak is clear, the evening peak is represented only by the small stubs in periods 2 and 3. As the wind dropped, rather abruptly, there was an upsurge in numbers of Trichoptera taken. This catch is one of the most useful of all catches taken. It will be noted that in fig. 5 the plotted position of 18-19 July is one of the poorly correlated catches. If the evening had been 'normal', wind being low or absent, the point would probably have been located well to the right.

Wind on the night of 16-17 June varied from 17 to 22 mph and the pattern is clear (fig. 3). It varied from 13 to 18 mph on 23-24 July and the pattern appeared. On 1-2 August the wind varied from 2 to 8 mph, but the temperature fell 14°F; the pattern is obscured by fluctuations between the peaks. Thus, if the effect of wind be removed, it is seen that temperature plays a major role in determining flight activity. The fact that most Trichoptera species fly *en masse* at night and not during the day when temperatures are higher, suggests an inhibiting effect of either or both of temperature or light. Wind can only make it difficult, or impossible, for the insects to fly, and thus to come to the trap, no matter how much they may be encouraged to fly by high temperature. The pattern will remain clear but numbers will be reduced. Thus wind and



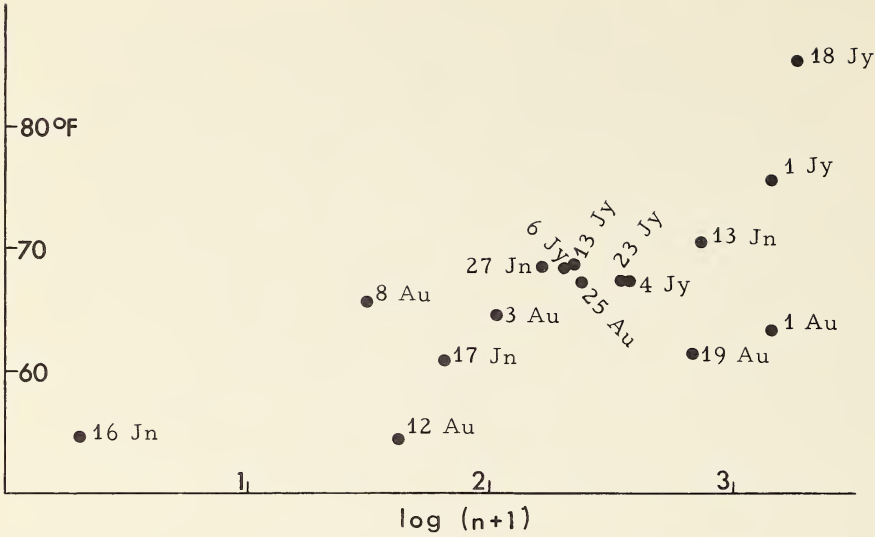


Figure 5 - Mean night (plus sunset & sunrise periods) temperature plotted against mean log (n + 1) of the hourly catch of Trichoptera.

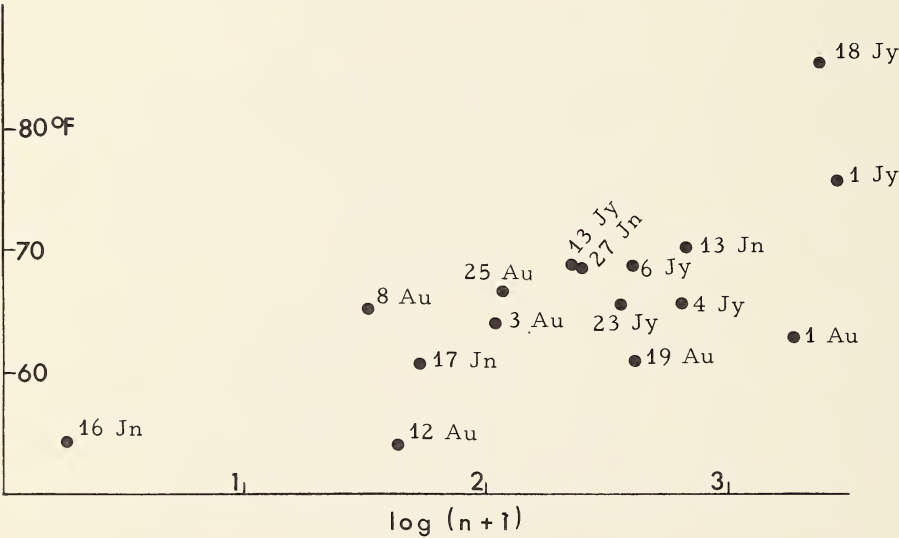


Figure 6 - Mean night (inter-peak) temperature plotted against the mean log (n + 1) of the hourly catch of Trichoptera.

temperature seem to be major factors in determining the overall catch for any one night. But the peaks, barring such exceptional circumstances as occurred on the night of 18-19 July, will remain detectable.

*The periods between the peaks* - To determine more precisely the effects of environmental factors the peak period data must be omitted from consideration, and the inter-peak periods examined more closely. The periods involved here are numbers 3 to 7, 3 to 8, or 3 to 9, depending on the time of sunrise.

Saturation deficit is not considered as it fluctuates from one hour to the next, with no apparent correlation with Trichoptera numbers. Figs. 6 and 7 illustrate mean  $\log(n+1)$  plotted against mean temperature and mean wind speed, for the appropriate sets of periods on collection nights. Fig. 6 shows a strong correlation of temperature with mean  $\log(n+1)$ . Wind speed (fig. 7) shows some negative correlation as expected, but this is obscured since wind is secondary to temperature. Figs. 6, 7, and 8 collectively demonstrate the role of wind in disrupting the effect of temperature on the flying population. Fig. 8 gives mean  $\log(n+1)$  plotted against mean temperature times mean wind speed. It will be seen that the distribution of nights is similar to that of fig. 7; as temperature is also involved, the vertical spread in fig. 8 is slightly greater than in fig. 7. In fig. 6, showing mean  $\log(n+1)$  against mean temperature, the distribution is entirely different, and the correlation is much improved, and positive. This is further evidence of the overriding effect of temperature and the subsidiary disrupting effect of wind on flight of Trichoptera in the time between the peaks.

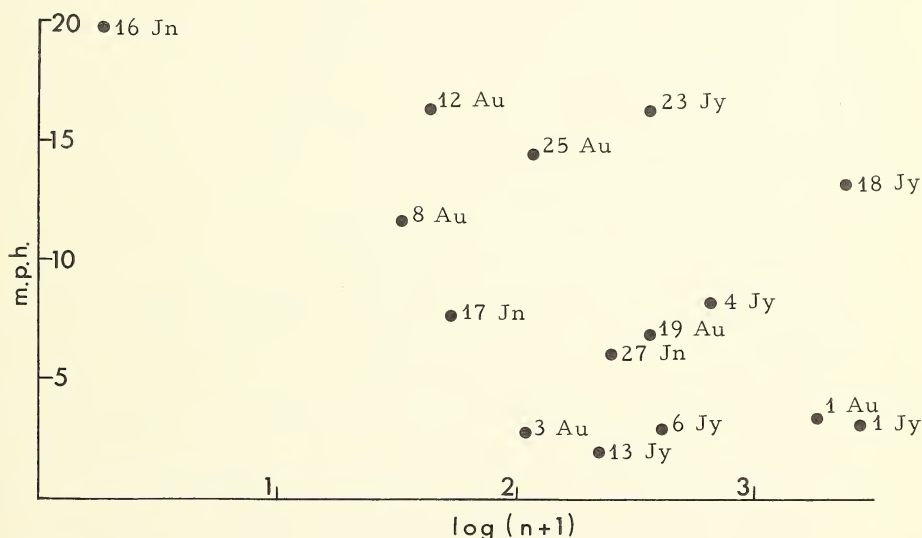


Figure 7 - Mean wind speed against mean  $\log(n+1)$  of inter-peak catch of Trichoptera.

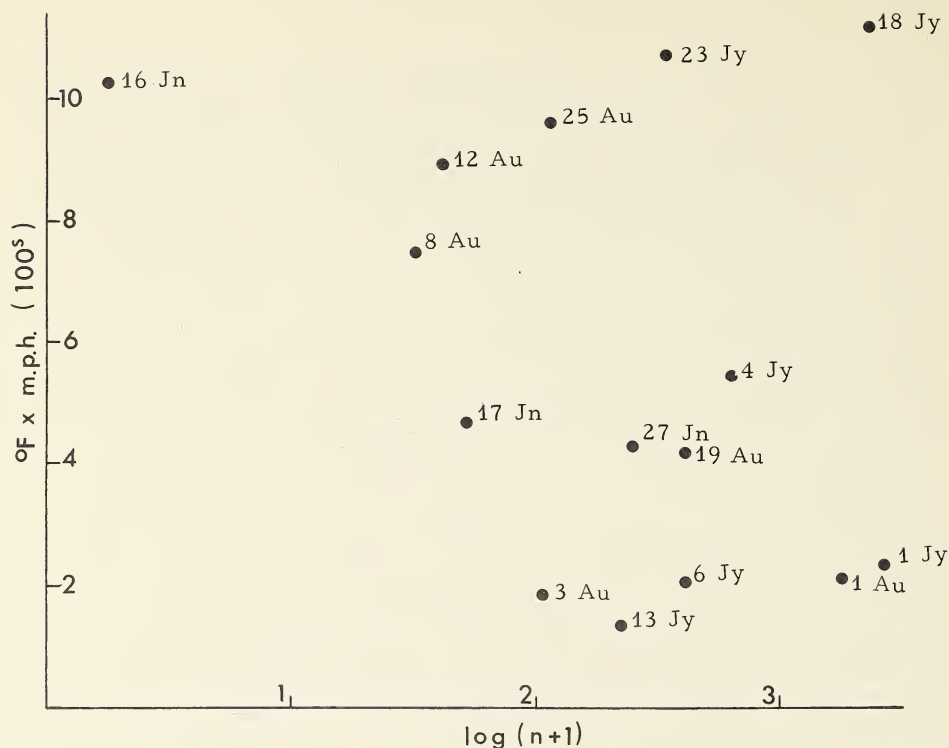


Figure 8 - Mean temperature X mean wind speed against mean log (n + 1) of inter-peak catch of Trichoptera.

Fig. 9 presents log (n + 1) plotted against temperature for each separate period, as limited in this section, for all catch nights. Again a definite correlation is seen, in more detail. The crosses represent the 5 catches from the night of 18-19 July and it will be observed that periods 3, 4, and 5, before the wind dropped, show low catches relative to the rest of the scatter.

In a statistical analysis of the data from inter-peak periods, the method of multiple correlation as set out in detail by Croxton & Cowden (1955) was used. Values of log (n + 1) are designated in the following as  $X_1$ ; of temperature,  $X_2$ ; of wind speed,  $X_3$ . Details of the calculations are omitted, suffice it to summarize the results,  $X_1$  being the dependent variable:

Using one independent variable:  $X_2$  or  $X_3$

Total variation of $X_1$ ,	$\Sigma x_1^2 = 69.7634$
Variation explained by use of $X_2$ only	$= 32.4282$
Standard error of estimate	$= 0.6789$
Coefficient of correlation,	$r_{12} = +0.6817$

Thus variation in temperature serves to explain 68% of the variation in log (n + 1), or 68% of the changes in numbers are associated with changes in temperature.

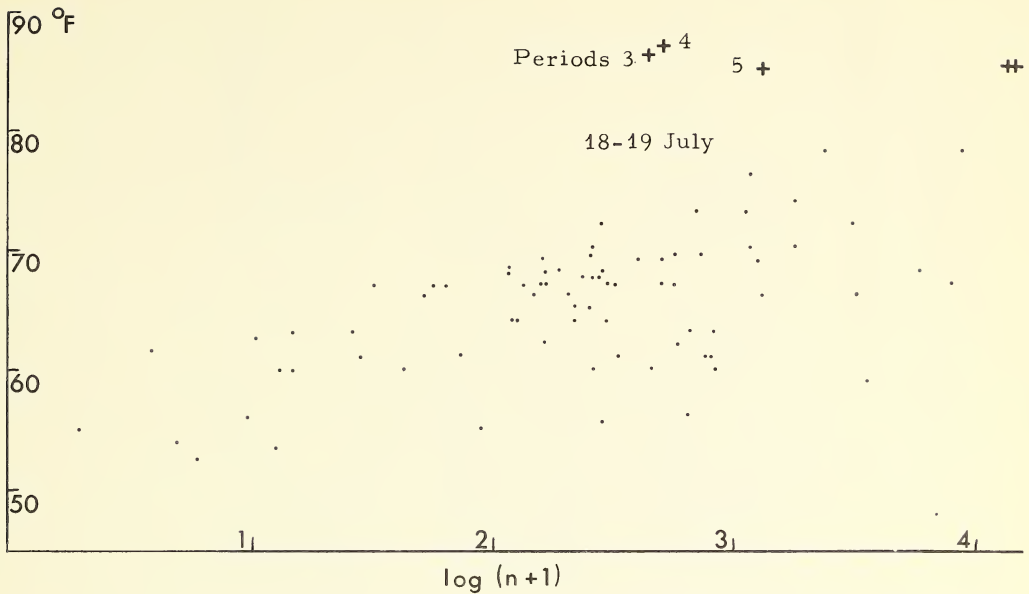


Figure 9 - Temperature against numbers of Trichoptera (as  $\log (n + 1)$ ) taken at an ultra-violet light trap at Ile Ste. Hélène, Montreal, summer 1964. Each 1 hour inter-peak period for all catch nights plotted separately.

Variation explained by use of $X_3$ only	= 14.3372
Standard error of estimate	= 0.8272
Coefficient of correlation	= -0.4533

Thus variation in wind, serves to explain 45% of the variation of  $\log (n + 1)$ ; i.e. 45% of the changes in  $\log (n + 1)$  are associated with changes in wind speed.

Using two independent variables:  $X_2$  and  $X_3$

Total variation,	$x_1^2$	= 69.7634
Explained variation,	$x_{c.23}^2$	= 39.6811
Coefficient of correlation,	$R_{1.23}$	= +0.7541

Thus temperature and wind speed together account for 75% of the variation of  $\log (n + 1)$ ; i.e. 75% of the changes in  $\log (n + 1)$  are associated with changes in temperature, wind speed, or both.

As the combined effect of these two factors on numbers of insects taken is to the extent of 75%, the interaction of temperature and wind may be assumed to be 38% (i.e.  $45 - (75 - 68) = 38$ ). The remaining 25% of variation may be attributed to saturation deficit and other unmeasured and unrecognized factors. An application of the F test for the reliability of  $R_{1.23}$  shows this to be clearly significant, that is, the correlation between  $X_1$ , and  $X_2$  & 3 appears to be very good.



*The pattern at the species level-* For each species the graphed pattern of only one night is used as the species patterns follow the total numbers pattern closely. The night chosen for each species was that which showed the pattern most clearly. Varying seasonal occurrence prevented the same night being used for all species, but only two nights were needed: 13-14 June and 25-26 August. Species and night are given in fig. 10. It will be seen in these graphs that all seven species tend to follow the pattern, with differences, of course, but these are minor.

Included in fig. 10 are 2 additional graphs, for *H. recurvata* and *C. speciosa*. They are both for the night of 18-19 June on which the speed suddenly decreased. In these two figures an evening peak is discernible, especially in *H. recurvata*. The overall depression of the first half of the night shows, but the species numbers rose to a peak, then fell away; the wind dropped and the numbers recovered to the assumed 'normal' for that night. On this night *Athripsodes cancellatus* also showed a peak, but not so well. The interesting point here is, that it was the three large species (body length > 4 mm) which produced discernible evening peaks of flight activity despite the high wind. Three other species, *Psychomyia flavida*, *Protophila maculata*, and *Hydrophila spatulata*, showed no evidence of a peak at all: they are all micro-Trichoptera. Thus size is seen to be of importance to a species in maintaining the pattern of night time activity, if winds are high and fluctuating. This diversity due to size may well be another factor in the 25% variation in  $\log(n+1)$  remaining to be explained.

In fig. 4 are graphs of the patterns using mean values of  $\log(n+1)$ . Allowance should be made for sunrise shift.

#### *Sex Ratios*

Sex ratios were examined to determine if the sexes were active at different times. In all seven species considered in detail, at least fifty per cent of the total numbers of each night arrived by period three. In most cases the ratio is about 50 throughout the night.

It seems safe to conclude that the pattern of total numbers of Trichoptera taken at light is due neither to any one sex of any one or more species, nor to any species as a whole.

#### *Ten Minute Catches - Total Numbers*

Fig. 11 shows patterns for individual nights using  $\log(n+1)$  values, and fig. 12 shows the average pattern for the summer, using mean values of  $\log(n+1)$ .

The points to observe are as follows. For the first six periods there were no catches or, at most, small numbers: occasionally catches in periods 4 to 6 were substantial. The peak of flight activity generally occurred in catch period 7 but sometimes in period 6, 8, or even 9.

From figs. 11 and 12 it will be seen that the peak follows immediately after civil twilight. Fig. 13 shows that a sharp change in rate of decline of light intensity occurs at civil twilight.

The curve of activity generally starts to rise prior to civil twilight, indicating a response either to low, or a lowering of, light intensity. However, the sudden upsurge to the peak seems to be associated with the sudden change in rate of decline of light at civil twilight. Harker (1961)

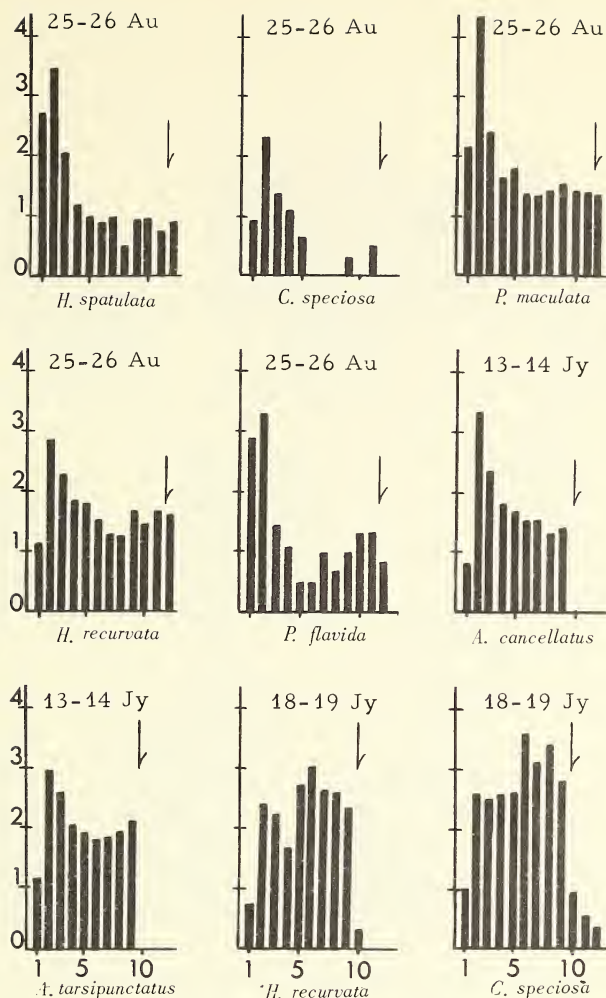


Figure 10 - Pattern of arrival on selected nights of seven species of Trichoptera at a UV light trap at Ile Ste. Hélène, Montreal, summer 1964. Two additional graphs are included for reasons given in the text. Abscissae in 1 hr periods, ordinates numbers as  $\log(n+1)$ . Sunset coincident with the first period mid-point. Sunrise indicated by arrows.

points out that "... it is rare for activity to occur as an immediate reaction to change in light intensity". It could be, therefore, that the peak is a delayed reaction to the light values of earlier periods, which are themselves vastly lower than normal daytime values. Nielsen's (1963) summary of the situation in poikilotherms: "The releasing factor may be a certain low level of illumination, or it might be a certain rate of change of intensity or a combination of both" seems appropriate to the uncertainty concerning the role of natural light in producing the peaks in Trichoptera. One further possibility is that the change in the rate of decline of light intensity induces an immediate increase in flight activity.

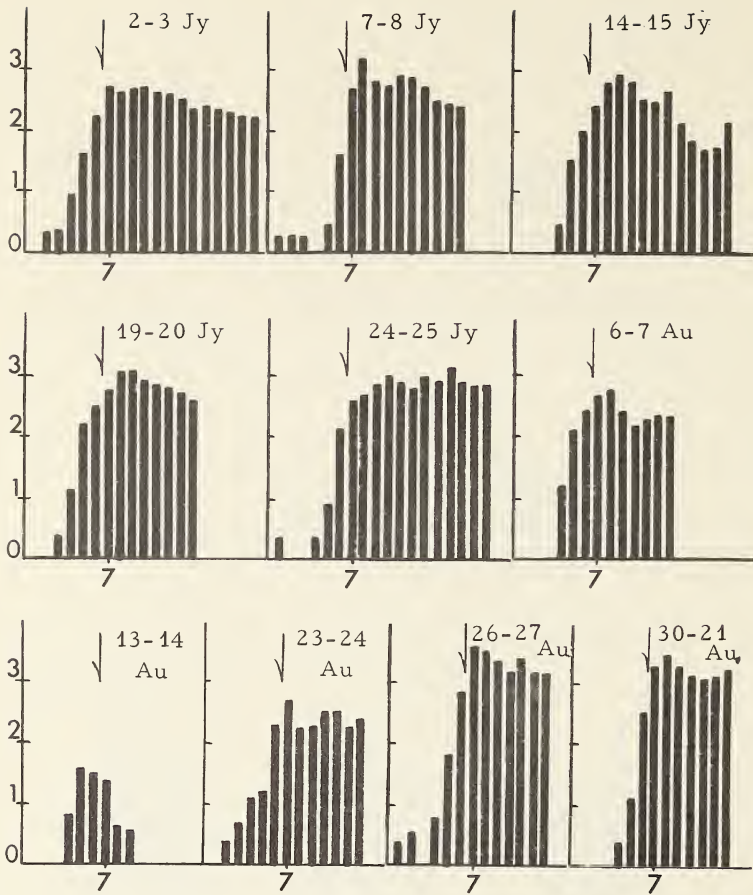


Figure 11 - Total number of Trichoptera taken at a UV light trap at Ile Ste. Hélène, Montreal, summer 1964, for each night on which 10 min catch periods were used. Ordinates in  $\log(n+1)$ , abscissae in 10 minute periods, log values plotted at the period mid-points. Civil twilight indicated by the arrows.

## DISCUSSION

### Previous Studies of Nocturnal Activity Patterns in Trichoptera

Light trap studies of the nocturnal flight activity rhythms of insects of immediate interest, are those by Williams (1935 and others), Stage & Chamberlin (1945), Southwood (1960), Corbet and Tjønnealand (1955), and Brindle (1957 a, b, and 1958). Most papers mention Trichoptera in passing, if at all. Trichoptera have been studied seasonally (Crichton 1960, Marshall 1939), rather than hourly, as here; such studies are consequently of little interest in the present context. It is unfortunate that there appear to have been no studies of Trichoptera using non-attractive traps, other than that of Lewis & Taylor (1965).

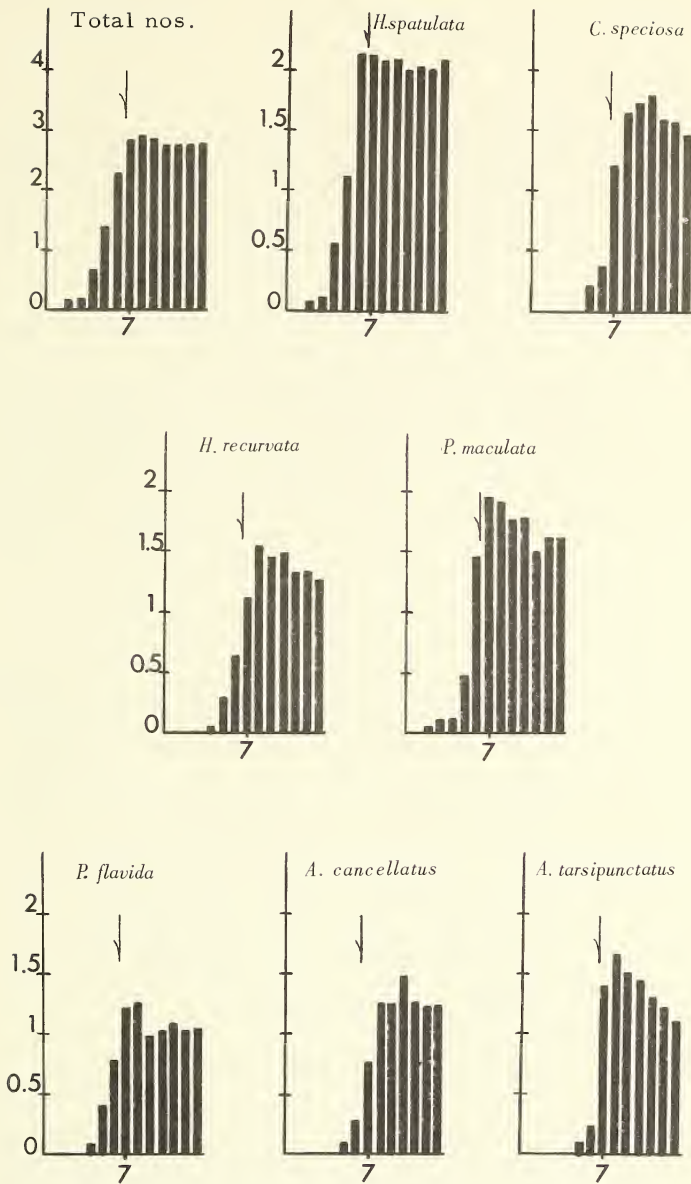
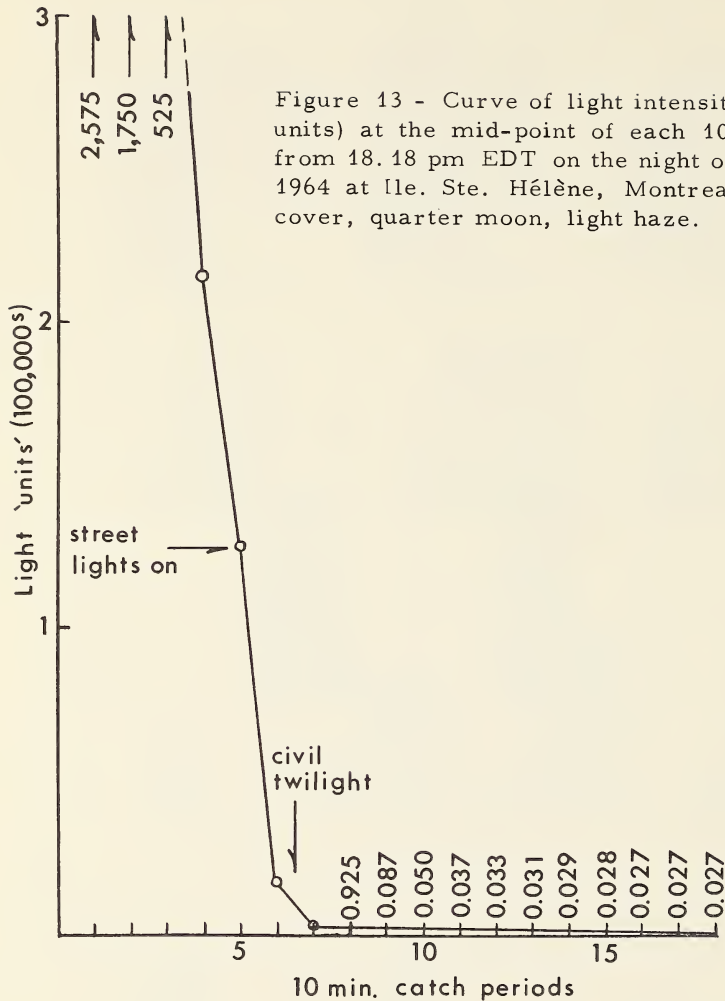


Figure 12 - Means of numbers of Trichoptera taken per 10 min period at an ultra-violet light trap at Ile Ste. Hélène, Montreal, for those equivalent periods of each night on which trapping was carried out, summer 1964. Abscissae in 10 min periods, ordinates in  $\log(n+1)$  with values plotted at period mid-points. The arrows mark civil twilight.





#### The Pattern at Montreal

The pattern found in this study has the following characteristics: bimodal, the evening peak relatively much more pronounced than the morning peak; the pattern of numbers in periods exclusive of the peaks forms a gradually decreasing slope from the evening peak till the slight rise to the morning peak; the interpeak slope may be punctuated by fluctuations of varying degrees, dependent on meteorological factors; the morning peak is terminated by an abrupt drop-off in numbers to zero, or almost zero. Referring to Corbet & Tjønneland's (1955) classification of relative development of the two peaks in East African Trichoptera, the present 7 species seem to fit their class 2 well; "Both peaks discernible, dusk peak far more pronounced".

### Meteorological Factors and the Pattern

The day-to-day effects of temperature and wind were dealt with here only superficially, for two reasons: 1). The paucity of data did not warrant any emulation of, for example, Williams' work on Lepidoptera (1961) and Simuliidae (1962) in this respect and, 2). this was not the purpose of the study. The analysis here was done simply as a step towards examination of the inter-peak fluctuations, and to aid in determining the role of light. The gross effect of temperature and wind on magnitude of the total catch on any one night has been demonstrated and Williams (1961) says that "The activity of insects on any one night is very largely determined by temperature and wind, ...". Brindle (1957a) mentions the effect of wind on two night's catches. Each night the wind was from a different quarter: once from a river, once from a reservoir. The species composition differed remarkably on these nights and corresponded with the fauna of the source from which the wind blew. One species was common to both nights however, but not to both habitats, "... a strong flyer" as Brindle says and, being a species of *Phryganea*, it is a 'large' trichopteran. This, again, agrees with the evidence from the night of 18-19 July, for the differential effect of wind depending on insect size. Brindle also examines the effect of temperature and relative humidity and finds higher temperatures, associated with lower relative humidity, better for larger catches. It is uncertain how he regards relative humidity, but certainly there is agreement on temperature effects. My determination of temperature and wind as prime factors in determining the total catch of any one night is in general agreement with the few papers which deal specifically with Trichoptera activity patterns and weather, and with Williams' (1961) statement.

### The Role of Light Intensity

The role of natural light in producing the peaks in numbers taken at dusk and dawn at artificial light, has previously been examined only by Corbet & Tjønneland (1955). They concluded that flight is inhibited by light above a certain intensity. At intensities below this light is conducive to mass flight activity; at still lower intensities flight activity dwindles but does not cease entirely. They speculate that activity is positively correlated with light intensity, up to the inhibiting value, but do not explain why flight occurs when it is almost dark, as between the peak periods.

It has been shown here that the evening peak was preceded by a sharp upsurge from zero, just prior to civil twilight. The sharp drop-off after the morning peak seems to mirror the sharp rise before the evening peak. Detailed examination of the morning peak may be expected to show that the sudden drop occurs very close to but after morning civil twilight, as found by Corbet & Tjønneland in Africa. One possible explanation for the relative insignificance of the morning peak may be found in the fact that light is increasing, rather than decreasing. I have suggested that the evening peak is triggered by a certain light value, but that all that is needed for night activity, is light lower than a certain intensity (see fig. 13). If this is so, the increase in light in the morning prior to attainment of the crucial light intensity, should have little effect on the numbers taken. Then, when the critical intensity occurs, little time will be avail-

able for a peak to develop as the conditions of full daylight which follow inhibit flight.

#### Meteorological Factors and the Inter-Peak Periods

A pattern of steadily but gradually decreasing numbers between the evening and morning peaks appears to be usual at Montreal and resembles that described by Corbet & Tjønneland (1955). Meteorological factors play a vital role in determining the level of the pattern provided their action is steady or non-violent throughout the night. However, the inter-peak pattern will reflect any sudden changes in meteorological factors.

Corbet and Tjønneland ran their trap on nights in which the meteorological factors varied little from night to night, or within nights. Thus they had no opportunity to determine the effect of fluctuations on their catches. They used 10 min catches throughout the night and those of their species which showed patterns similar to the one here, but much more clearly, showed a certain amount of fluctuation between the peaks which is not directly attributable to any factors considered here, and can probably be labelled intrinsic. But though they experienced only light breezes they did demonstrate the differential effect of wind on species of various sizes; they did not relate wind directly with pattern fluctuations, but appear to have done so indirectly. Thus part of the apparently intrinsic variation may have been due to light wind and small species.

#### Natural Affinities of the Pattern

To determine the actual daily flight activity pattern of Trichoptera, some trapping method is required which collects independently of any response on the part of the insects (e.g. Lewis & Taylor 1965). It seems reasonable to suppose that, in species showing a bimodal activity pattern such as were worked with here, the pattern *between* the tips of the peaks is a reflection of the natural pattern. The gradual decrease from the usually much larger evening peak, towards the morning peak is ignored for the present. The point is that a certain basic level of activity appears to be demonstrated between the peaks. Whether this is the same level as the daytime flight activity level, or higher or lower, cannot be said. But daytime flight is not uncommon in Trichoptera (Brindle 1957a, Peterson 1952, Lewis & Taylor 1965). Daytime flight, especially in late afternoon was frequently observed in several species at Ile Ste. Helene. Swarming activity, especially by *H. recurvata*, was common. So it may be, in some species, that the nighttime level may be the low point of the 24 hour period, and the peaks the result of inducement to still greater activity. But most species generally only *appeared* flying after sunset. Some lack of response to the mercury vapour light may explain part of the abrupt rise and fall in evening and morning, but as the change from twilight to full sunlight, is gradual, so also should the decrease in attractiveness of the light be gradual, which it is not. But from just what level of a flying population the evening rise, for example, is abrupt, cannot be deduced here. Considering the day activity of some species, the abrupt rise may be explained by the light gradually becoming effective when the flying population is already at a high level. However, the peaks, as such, above this level, can only be regarded as natural phenomena in themselves, due to the gradual decrease after the evening peak and the slight rise pre-

ceeding the morning peak.

Another point which may support the 'natural' peak is the spectral quality of the light source (see table 1 p. 220). Emitting largely in the short wavelength end of the spectrum, the bulb should appear in daytime as a discrete source of stronger radiation of these attractive wavelengths. The smaller numbers of insects taken in the trap in daytime may be attributed in part to competition of daylight with the trap light source and in part to less activity. In a way, therefore, the use of a mercury vapour light source may actually provide a preliminary guide as to whether or not the pattern is natural. It is proposed that, in its essential features, it is, for those species which exhibit it.

#### ACKNOWLEDGMENTS

I wish to thank the Canadian Corporation for the 1967 World Exhibition, Montreal, Quebec, for initiating the Shadfly Project, thus enabling this study to be carried out and providing the opportunity for me to meet and work with people of long experience in my fields of interest.

I am deeply grateful to Dr. P.S. Corbet, Entomology Research Institute, Ottawa, for his guidance in my part of the overall investigation, as here set out. I am indebted to Mr. J. Lafrance, Canada Department of Agriculture Laboratory, St. Jean, Quebec, for very kindly loaning the mechanical trap. To Dr. W.G. Evans, Dr. B. Hocking, and Dr. R.C. B. Hartland-Rowe, I extend many thanks for their critical reading of the manuscript, subsequent guidance, and many useful suggestions. I thank Mr. E.E. Miles, General Electric Co., Oldham, Lancs., England, for the information on the mercury vapour spectrum.

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## AN ANNOTATED LIST OF THE FORMICIDAE (HYMENOPTERA) OF CENTRAL AND SOUTHERN ALBERTA

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Quaestiones entomologicae  
2:243-253 1966

*Forty species of ants are recorded in Alberta, with notes on their distribution in the province. The presence of large numbers of the frog Pseudacris triseriata Agassiz in a nest of Formica ulkei Emery is reported.*

Ants were collected all over the region of Alberta southwest of a line between Peace River and Vermillion. No collecting was done on the Alaska Highway north of Peace River; the only other accessible area which was not studied lies between Smoky Lake and Cold Lake. An extensive collection was made in the summer of 1963 and the material was supplemented during shorter field trips in 1964 and 1965. Twenty one numbered ecological areas in the province of Alberta were defined by Strickland (1951). An ant species is recorded as occurring in an ecological area if it is generally distributed throughout that area. Strickland's numbering is used.

Most species were first identified using Creighton's "The Ants of North America" and the original sources referred to by Creighton; Emery (1893, 1895), Gregg (1963) and several works by W.A. Wheeler, were also useful. It was found that most albertan species occur in North Dakota. The determinations were then checked with the excellent descriptions in Wheeler and Wheeler "Ants of North Dakota" (1963). There are 82 indigenous species of Formicidae in North Dakota and 36 of these are also found in Alberta. Another two albertan species (*Formica impexa* and *Manica hunteri*), which do not occur in North Dakota, are distinguished in Wheeler and Wheeler's well illustrated keys. Of the 40 species here recorded for Alberta only 2 species (*Formica subpolita* and *Formica hewitti*) cannot be identified using "The Ants of North Dakota". Of 54 species of ants occurring in British Columbia (G. Ayre pers. com.) only 22 species are shared by Alberta.

My thanks are due to Dr. W. L. Brown, Cornell University, and Dr. E. O. Wilson, Harvard University, for assistance with determinations. I also thank Miss C. A. Sharplin who spent 3 weeks of her 1963 vacation collecting ants.

### ECOLOGICAL AREAS IN ALBERTA

The map and descriptions of ecological areas are adapted from Strickland (*in* Bowman 1951) with the help of G. H. LaRoi and J. Packer.

*Transition Zone*

1. *Cypress Hills* - About 50% forested; lodgepole pine, spruce, aspen, and willow; remainder, long grass. Very little cultivation. Elevation up to 4500 ft. Soil; very dark brown. Summit of hills, an extensive tableland which never glaciated. Rainfall 10-11.4 in. Flora and fauna very similar to those of area 18.

2. *Southern Prairie (dry) (Medicine Hat)* - Short grass. A few poplars, willows, and a variety of bushes in river bottoms; cactus and sage are common, a few yuccas found in the extreme south. Crops: chiefly grain. Deserted land; mustard and Russian thistle. Soil, fine brown clay, sandy in eastern half. Rainfall less than 10 in.

3. *Southern Prairie (about 50% irrigated) (Lethbridge)* - Resembles area 2. Vegetation on dry areas similar, but irrigated parts carry a greater variety of crops, alfalfa and beets predominate. Both soil and rainfall are a little heavier.

4. *Northern Prairie (East) (Steveville)* - Short to moderate long grass; much deserted land. Crops: almost entirely grain. Soil; dark brown loam. Rainfall less than 10 in. Very light in eastern half.

5. *Northern Prairie (West) (Drumheller)* - Moderately long grass. Crops: grain. Soil; heavy clay "gumbo" to dark brown loam. Rainfall, 10-11.5 in.

6. *Northern Prairie (Southwest Extension) (Calgary)* - Moderately long grass, occasional groves of willow and aspen. About 60% under cultivation. Crops: grain and hay. Soil; dark brown loam. Rainfall, 10-11.5 in.

*Intermediate Between Transition and Canadian Zones*

7. *Parkland (East) (Lloydminster)* - About 30% wooded; aspen and willow groves, most heavily in northern half; remainder, moderately long to short grass. Crops: grain and some hay. Soil; dark brown loam; some areas almost pure sand. Rainfall less than 10 in.

8. *Parkland (West) (Red Deer)* - Originally about 50% wooded; mainly aspen; remainder, long grass; now about 70% cleared. Crops: grain and hay, Soil; dark brown loam. Rainfall 10-13 in.

*Canadian Zone*

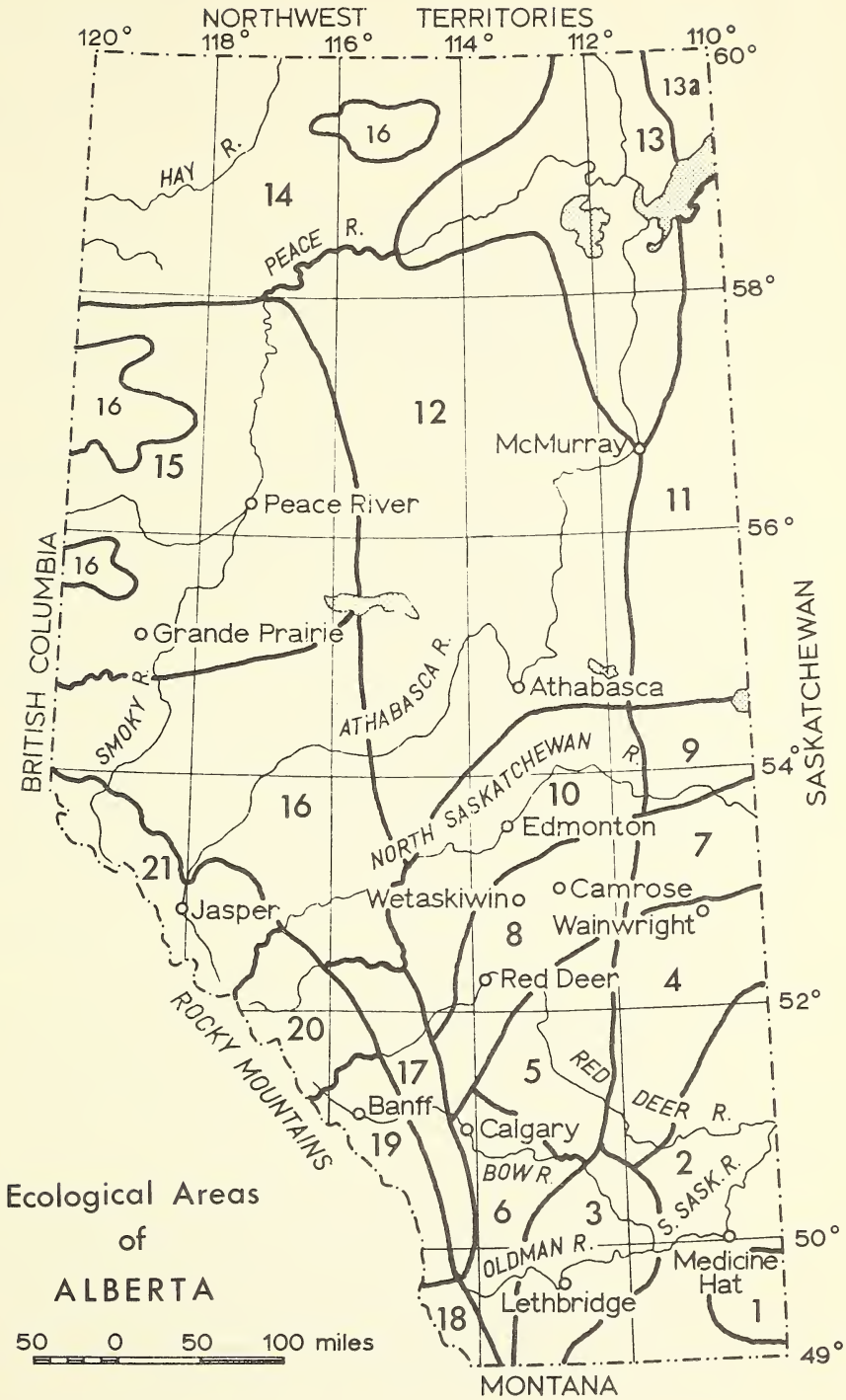
9. *Poplar (East) (Saint Paul)* - Originally, aspen, balsam poplar, and willow, with some spruce; less than 50% cleared. Crops: chiefly oats. Soil; black loam. Rainfall about 10 in.

10. *Poplar (West) (Edmonton)* - Vegetation, as no. 9, larger local stands of spruce and pine; about 70% cleared. Crops: wheat and oats, some hay, particularly clovers. Soil; black loam, with high humus content. Rainfall over 13 in.

11. *Mixed Forest with Eastern and Subarctic intrusions* - Poplar, spruce, pine, fir, tamarack, willow, birch, and alder. Soil; gray wooded, large areas of sand. Rainfall, probably 10-11 in.

12. *Mixed Forest with Cordilleran (Rocky Mountain) intrusions (Fawcett)* - Similar to area 11; numerous lakes and large areas of muskeg. A little cultivation in the south. Crops: chiefly oats. Soil; gray wooded, very variable in texture. Rainfall, 11.5 to over 13 in.

13. *Mackenzie lowlands* - Mixed forest, as no. 11, more Alpine - arctic species; long grass and sedges in open spaces. No cultivation. A small





area (13a) of subarctic woodland extends into NE corner. Soil, probably all gray wooded.

14. *Mixed Forest with some Parkland and Alpine-Artic intrusions* - Vegetation resembles nos. 12 and 15. No cultivation.

15. *Mixed Forest and Parkland (Beaverlodge)* - Large mixed forest areas interspersed with long-grass open plains. Crops: chiefly grain and hay. Soil; 10-15% black loam; much gray wooded, scattered patches of sand. Rainfall, 10-13 in.

#### *Foothill Zone*

16. *Foothills (Northern) (Edson)* - Vegetation merges from that of no. 11 to that of 21. Some hay and grain in eastern half. Soil; gray wooded. Believed to be very variable. Rainfall over 13 in.

17. *Foothills (Southern)* - Aspen, spruce, lodgepole pine, and willow, with much open prairie towards the southern end. Soil; gray wooded in north merging to dark brown in the south. Rainfall, 13 in. in northern part but less than 10 in. in south.

#### *Mountain Zone*

Vegetation - This varies greatly. Montane territory is dominated by lodgepole pine and white spruce. Douglas fir is locally abundant. Subalpine territory is characterized by Engelmann spruce, alpine fir, and other conifers, as well as by mountain heaths.

From area 18 to area 21 there is a gradual replacement of southern and western species by certain boreal and arctic species.

18. *Southern Rocky Mountain (Waterton and Crow's Nest Pass)* - Strong intrusions of southern and western species extend to about the northern limits of this area. Soil; has a higher lime content than have the more northern mountain areas. Rainfall over 13 in.

19. *Central Rocky Mountain (Banff)* - Vegetation typical for entire mountain zone with few southern or Arctic intrusions. Soil; though very variable is, generally speaking, of a gray wooded type. Rainfall over 13 in.

20. *North Central Rocky Mountain (Nordegg)* - Vegetation similar to that of 19 but the late Dr. Malte, Dominion Agrostologist found several species of grasses which had been considered as confined to Labrador growing in the vicinity of Nordegg. Soil and rainfall as in area 19.

21. *Northern Rocky Mountain (Jasper)* - Vegetation, soil, and rainfall as in no. 19, but with strong intrusions of arctic and boreal species.

## SUBFAMILY MYRMICINAE

### **Genus *Myrmica* Latreille (Weber 1950)**

*Myrmica brevinodis* Emery - Is a very common ant in areas 1, 5 to 8, 10, 12, and 15 to 21. It is found up to timber line in the Rocky Mountains. Several collections were made in Jasper Park around 7,000 ft. In the drier south-central and southeastern part of the province *M. brevinodis* is less common, being found only in wooded areas or near water.

*Myrmica brevispinosa* Wheeler - Several nests of this species were found in area 10, and one near Milk River (3 Aug. 1963).

*Myrmica emeryana* Forel - Was recorded twice only:- Devon 20 June 1963, and Lake Cardinal provincial park, west of Peace River, 14 Sept. 1964.

*Myrmica lobicornis fracticornis* Emery - Many records of this species were obtained in areas 1, 3, 4 to 8, 10, and 16 to 21. This ant was not found in the hot dry area around Medicine Hat.

#### Genus *Manica* Jurine

*Manica hunteri* Wheeler - Several nests were found at Gorge Creek in the foothills west of Turner Valley, 24 June 1965. One collection was made in Jasper Park at an elevation of 4,500 ft., Oct. 3 1964.

*Manica mutica* Emery - Was recorded in Alberta by E.H. Strickland but as his specimens are no longer available this record could not be verified.

#### Genus *Pogonomyrmex* Mayr

*Pogonomyrmex occidentalis* (Cresson) - Was found only in area 2. In this area the large mound nests and clearings are easily seen; the first nest found was spotted from a moving car on Highway 1.

#### Genus *Monomorium* Mayr

*Monomorium minimum* (Buckley) - One specimen was collected from a thistle leaf near Medicine Hat airfield on 6 Aug. 1963. The nest was not located.

*Monomorium pharaonis* (Linnaeus) - An infestation of "pharoah's ant" was recorded in a building in Lethbridge in 1946 by E.H. Strickland.

#### Genus *Leptothorax* Mayr

*Leptothorax muscorum* (Nylander) - (Brown 1955: L. (*Mychothorax*) *canadensis* Provancher in Wheeler and Wheeler 1963). This ant is common in the wooded areas of central and western Alberta.

*Leptothorax ambiguus* Emery - Was collected only once, at Celestine Lake, Jasper National Park, 24 July 1963.

### SUBFAMILY DOLICHODERINAE

#### Genus *Tapinoma* Forster

*Tapinoma sessile* (Say) - This tiny ant is found in an extraordinary

variety of habitats; Flatbush 23 Aug. 1963 in damp aspen woodland, near the Columbia Ice Field 26 July 1963 at an elevation of 6,400 ft., Writing-on-Stone provincial park 3 Aug. 1963 on the side of the Milk River Canyon, Steveville 7 Aug. 1963 in badlands, and in urban Edmonton. Although widely distributed, this ant is nowhere very common.

#### SUBFAMILY FORMICINAE

##### Genus *Camponotus* Mayr

*Camponotus herculeanus* (Linnaeus) - The large dark carpenter ant which is very common in the foothills and on the wooded slopes of the mountains. It is also common in the west central parkland. Numerous records were obtained in areas 10 and 15 to 21. A few records were obtained east of this line e.g.: Ardrossan 18 Aug. 1963, Tofield 22 Sept. 1965, Flatbush 1 June 1964, but *C. noveboracensis* was more common in these areas.

*Camponotus noveboracensis* (Fitch) - The red and black carpenter and which occurs in areas 7, 8 and 10. The most westerly record was Devon 20 June 1963, most southerly - Drumheller 8 Aug. 1963, and the most northerly - Flatbush 1 June 1964.

*Camponotus* (Myrmentoma) *nearcticus* Emery - Only one nest of this species was found. It was in a large, old fallen tree trunk in a small patch of woodland on the south bank of the Red Deer River 16 miles west of Drumheller, 8 Aug. 1963.

##### Genus *Lasius* Fabricius (Wilson 1955)

*Lasius alienus* (Forster) - This species is very common in the foothills, areas 17 and 18. It was found at every one of many stops in a 2-day drive down the forest road from Kananaskis to Coleman. *L. alienus* is abundant in the Gorge Creek area (collected June 24, 1965). Other records for this species are Waterton 3 Aug. 1963, Cypress Hills 5 Aug. 1963, Medicine Hat 6 Aug. 1963, Drumheller 8 Aug. 1963, and Opal 13 July 1963.

*Lasius neoniger* Emery - Is very common in open grassland, areas 2, 3 and 6. Little crater mound nests occur every few yards along the edges of paths and in the open where there is suitable light soil. *L. neoniger* was found in woodland near Elkwater 5 Aug. 1963. This species was also collected in sandy soil at Opal 13 July 1963 over 200 miles further north than the nearest record. Presumably it occurs in between.

*Lasius sitkaensis* Pergande - This species is common in area 10, and it was also found in sheltered habitats in the mountains, e.g. Lake Louise 28 July 1963. *L. sitkaensis* is not found in the open dry areas of the south-eastern region, but was taken in woodland in Kinbrook Island provincial park 6 Aug. 1963 and Elkwater 5 Aug. 1963.

*Lasius* (*Chthonolasius*) *umbratus* (Nylander) - Collected only at Lake Newell 6 Aug. 1963. This ant is probably rare in the province; no nests were found during a fruitless search for *Acanthomyops* in south central Alberta.

### Genus *Formica* Linnaeus

*Species belonging to the neogagates group* (Wilson and Brown 1955)

*Formica bradleyi* Wheeler - (subgenus *Proformica* in Wheeler and Wheeler 1963). The only record of this species is Medicine Hat 6 Aug. 1963.

*Formica lasioides* Emery (F. *Proformica lasioides*) - A nest of *F. lasioides* was found near Mount Eisenhower youth hostel on 28 July 1963. Most of the workers in this nest were about 5 mm long and had many erect white hairs on the scapes. Smaller specimens, between 3 and 4 mm long were collected from Opal 13 July 1963, Lake Newell 6 Aug. 1963 and Elkwater 5 Aug. 1963. Workers from these three localities had fewer erect hairs on the scapes.

*Formica neogagates* Emery (F. *Proformica neogagates*) - A few individual ants resembling small *F. lasioides* but lacking erect hairs on the scapes were found running on bare open ground in Dinosaur provincial park 7 Aug. 1963. The nest was not located.

*Formica obtusopilosa* Emery (F. *Raptiformica obtusopilosa* in Wheeler and Wheeler 1963) - This species occurs in the southern part of the province where it was collected from Milk River 3 Aug. 1963, Comrey 4 Aug. 1963, Steeveville 7 Aug. 1963, and Dinosaur Park 7 Aug. 1963.

*Species belonging to the sanguinea group which is also known as the subgenus Raptiformica* Forel

*Formica sanguinea subnuda* Emery - This slave-making species is very common and nests were found in all areas except 9, 11, 13 and 14 in which no ant collecting was done. *Formica fusca* is usually enslaved by this species, but many *sanguinea* nests without slaves were found.

*Formica subintegra* Emery - *F. subintegra* was recorded twice, from Elk Island National Park 14 June 1963 and Ministik Lake 18 Aug. 1963. *F. fusca* was the slave species.

*Formica puberula* Emery - This species was found only once, at Gorge Creek 24 June 1965.

Another species in the *sanguinea* group with a brown head and abdomen and a lighter thorax was collected from Medicine Hat. It could not be identified.

*Species belonging to the rufa group*

*Formica dakotensis* Emery (Brown 1957) - Is common in the foothills of areas 16, 17 and 20. Many nests were found along the Coal Branch Road between Nordegg and Edson (9-12 Aug. 1963). *F. dakotensis* is less common



further south in the foothills, but several nests were found near Kananaskis 1 Aug. 1963. It was collected at Peace River 15 Sept. 1964.

*Formica obscuripes* Forel - This species occurs all over southern Alberta, commonly in areas 1, 2, 3, 6, 17, 18, and 19. *F. obscuripes* makes thatched mound nests and the workers are conspicuously active, biting readily. It is a species that "cannot be missed" and therefore may appear to be more abundant than it really is. The nests were found on sunny grass slopes in the mountains and on open ground in the prairies. The most northerly record of this species in the province is Nordegg 9 Aug. 1963.

*Formica obscuriventris* Mayr - Three nests of this species were found: Mount Eisenhower 28 July 1963, Lake Minnewanka 30 July 1963, and Opal 13 July 1963.

*Formica oreas* Wheeler - One nest of this species was found in 1963 at Rainbow Valley, Edmonton. The site was revisited in 1964 and 1965 but no trace of *F. oreas* was found.

*Species belonging to the microgyna group*

*Formica impexa* Wheeler - Three nests of *F. impexa* were found in a sandy area on the east bank of the Athabasca River about 7 miles west of Flatbush on 23 Aug. 1963. In 1964 the nests were dug into in search of queens, which were not found, and the soil was replaced in the holes. In June 1965 the nests were found to be empty and only two individual *F. impexa* were found in the area. Perhaps this species is particularly susceptible to disturbance of the nest.

*Species belonging to the exsecta group*

*Formica opaciventris* Emery - Was found only once at Lucky Strike, 4 Aug. 1963.

*Formica ulkei* Emery - Is common in area 10. The large mound nests are conspicuous in clearings in woodland and along tree-lined trails. Sticky bud scales from poplars are usually littered over the mounds. Elk Island National Park affords excellent *F. ulkei* habitat. This species was found as far west as Edson 4 July 1963, and at Peace River to the north 15 Sept. 1964, but not in the mountains, in predominantly coniferous forest, nor on the open prairie.

In October 1965 40 frogs (*Pseudacris triseriata maculata* Agassiz) were dug from a sector of an active *F. ulkei* nest at George Lake, 53°58'N 114°05' W. After about one third of the mound had been dug out the frogs and soil were replaced. Two weeks later the nest was reinvestigated and no frogs or ants were found in the mound. Further digging revealed 20 frogs 2 feet below ground level; ants were also found in these deep galleries. After finding 20 frogs, I filled the hole in, but as frogs were turning up in every trowel-full of soil, it was assumed that there were more frogs below the 2-foot depth reached. No frogs were found in a control hole dug 10 feet away from the nest. *F. ulkei* is a vicious biter, but none of

the ants in this nest were attacking the frogs. Other mounds of *F. ulkei* were opened in the early spring of 1965 and in the fall of 1965 but no inquilines, frogs or insects were found.

*Species belonging to the fusca group.*

*Formica fusca* Linnaeus - Is the commonest ant in Alberta. It is found everywhere in the area studied except in area 2. It is, however, common in the Cypress Hills.

Three *F. fusca* nests at Devon were marked with stakes in the fall of 1963. During the first week of February 1964 the snow was cleared from these nests and they were dug out. In one nest ants were found in galleries 3 feet 6 inches below ground level. When warmed up these ants became active. No ants were found in the other two nests although the colonies became active again the following summer. It is probable that the ants were 4 ft. or more below ground level.

*Formica cinerea montana* Emery - (Gregg 1953) - Was found in three locations in the south of the province:- 5 miles northeast of Waterton 3 Aug. 1963, Lucky Strike 4 Aug. 1963, and Milk River 3 Aug. 1963. A nest of *F. cinerea* was also found on a south-facing embankment on the edge of a gravel road at Gorge Creek 24 June 1965.

*Formica neoclara* Emery - A common species in areas 16 to 21 inclusive. *F. neoclara* was also collected in Calgary in July 1964 and Drumheller 8 Aug. 1963.

*Formica neorufibarbis* Emery - Is the most common ant in the Rocky Mountain forests, areas 18 to 21. *F. neorufibarbis* varies in size and colouration with altitude. This phenomenon was studied between July 19 and 25 in Jasper Park in 1965. *F. neorufibarbis* is most abundant between 4,000 and 5,000 feet, but was collected above the tree line at 8,000 feet and in a valley at 3,400 feet. Large, well-established nests from different altitudes were compared. The majority of workers from the 6,500 to 8,000 foot level were between 6 and 7 mm long. The thorax of all workers was markedly lighter than the head and abdomen; 58 out of 317 individuals collected from the highest nests had a clear yellow thorax, the others had a yellowish brown thorax and yellow legs. The ants from nests found in the valley were smaller, 4.5 to 5.5 mm long. Twelve out of 357 had yellow thoraces, but some of these showed some infuscation of the nota. Many low altitude ants had a brown thorax, which although it was lighter than the head and abdomen did not give a bicoloured impression in the field. Intermediate forms occur at intermediate altitudes and I am convinced that only one species is involved, although the smaller, darker forms were confused with *F. marcida* Wheeler at first. *F. neorufibarbis* was also taken well away from the mountains at Sandy Lake, elevation about 2,000 ft., 5 June 1963.

*Formica subpolita* Mayr - Was recorded twice at Comrey, 4 Aug. 1963, and Medicine Hat, 6 Aug. 1963.

*Formica hewitti* Wheeler - Scattered records of this species were obtained, all from wooded areas:- Flatbush 23 Aug. 1963, Vimy 24 April 1964, Mount Edith Cavell 2 Oct. 1964, near Mount Eisenhower 28 July

1963, and Cypress Hills 5 Aug. 1963.

**Genus *Polyergus* Latreille**

*Polyergus rufescens* Latreille - This slave-making species was found in five large *Formica fusca* nests in different localities:- Devon 20 June 1963, Flatbush 23 Aug. 1963 (young queens were found in this nest), bank of Athabasca River 7 miles west of Flatbush 23 Aug. 1963 (winged males were present in this nest), Celestine Lake trail, Jasper, 24 July 1963 (dwarf *F. fusca* males were numerous in this nest), and Elk Island Park 10 July 1963.

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# A BATHYMERMIS SPECIES (MERMITHIDAE: NEMATODA) PARASITIC ON LARVAL TABANIDS

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A species of *Bathymermis* Daday 1911, is reported as a parasite of larval *Chrysops fuscata* Walk. Transmission of the parasite from infected soil to *Chrysops mitis* O. S. was accomplished in the laboratory. The parasitic larvae were reared from the hosts. The pathology of the mermithid is described and its possible use as a means of biological control for tabanids is discussed.

Larval tabanids were collected during 1958-1961 from the following three areas in Alberta: Winterburn swamp, 8 miles west of Edmonton; a grassy lake at Raymond and Welling, south of Lethbridge; two irrigation ditches near Waterton. The nematodes were first encountered during the spring of 1959. Since then all collections were examined for infected larvae. These groups of larvae were maintained individually in separate vials containing moist soil from their respective habitats. The larvae were of several species and ranged from 10-30 mm long. Natural infection was present only in *Chrysops fuscata* Walk. and from only one of the collecting sites (Table 1). Usually only one parasite was obtained from a single larva although up to five were recorded.

TABLE 1 - Incidence of *Bathymermis* sp. in larval tabanids in Alberta, Canada, 1958-1960.

Species - Place	Date	No. Infection %		Date	No. Infection %	
<i>C. fuscata</i> Winterburn	Oct. 1958	2	-	Jun. 1959	150	23
	Aug. 1959	78	27	Jun. 1960	156	28
	Jul. 1960	125	16	Aug. 1960	20	35
	Sept. 1960	16	37			
<i>T. reinwardtii</i> , Raymond & Welling				Oct. 1958	70	-
<i>C. mitis</i> , Vauxhall	Sept. 1959	183	-	Oct. 1960	221	-
<i>C. mitis</i> , Waterton	Sept. 1959	125	-			

Usually the nematodes were separated from the host's tissue and fixed in hot 70% alcohol with 5% glycerine for further study; more rarely



hot formalin was used as a fixative. Living specimens of the parasite after emergence from the host's body and from the soil were either examined alive or after clearing with glycerine and lactophenol. The salt flotation technique (Chandler 1952) was often used for soil examination for the nematode eggs.

It was usually noticed that when larval *C. mitis* O.S. were maintained in the soil collected from the Winterburnswamp area, they suffered from the nematode parasites. Two healthy batches of ten *C. mitis* larvae were maintained in the infected soil. About 70% of these larvae developed infection which became apparent after about 23 days.

#### NOTES ON THE LIFE-CYCLE AND PATHOLOGY

Dead larvae with signs of recent parasitisation were most numerous in early July. Emergence, however, continued until September, as parasitised larvae were still available then.

Several nematodes were seen to emerge head foremost either through the thoracic segments or the last abdominal segment of the host though emergence from the side of the abdomen was not infrequent. The parasites usually freed themselves in a few minutes. Immersion of the host in tap water and a room temperature of 70 F, hastened the emergence of the parasites which always resulted in the death of the host larva.

Although no field observations were made, it is assumed on the basis of the two main types of life-history in the Mermithidae, that the parasites on emergence undergo a last moult, copulation takes place in the soil and eggs are laid which hatch during the warm spring weather. After hatching, the larvae work their way into the host where they undergo further development. During the present study, in few preparasitic stages of the nematode larvae were observed to enter through the fleshy pseudopods of the host.

Mermithid eggs as described by Filipjev and Stekhoven (1941), and Christie (1937), were not seen in about 300 slides prepared with the infected soil for determination of the egg structure. Nevertheless, eggs bearing a close resemblance to the one described by Cobb (1926), were regularly obtained from the infected soil. These eggs and the subsequent free-living stage of the parasite although recorded during the present study are not described pending further examination and rearing to the adult stage.

Larval *Chrysops* are of yellowish-green colour, during early parasitisation this changes to pale-yellow and then black. Parasites could be easily seen in the mature larvae which became transparent owing to the absence of fat body and other tissues, revealing the white coils of the worms. In the immature larvae, the presence of the parasites could only be determined through dissection. Mature larvae were arrested in their development and failed to pupate. Infected larvae did not usually feed and were more sluggish in their movements than normal larvae.

#### NOTES ON STRUCTURE AND BEHAVIOUR

The largest specimen obtained was 29 mm and the mean length based on 20 specimens was 26.8 mm. Nematodes in multiple infections were

shorter than those of single infections. The following characters were recorded: tail often obtuse, short and conical. In two specimens which survived under laboratory conditions partly buried in the soil for about five months after emergence from the host larvae the spicula were parallel-sided; body colour white due to fat and storage tissue; cuticle smooth and composed of a number of layers; transverse striations present; head portion hemispherical, with six papillae; two amphids present; buccal opening terminal and buccal spear present.

On emergence from the host larvae the parasites were extremely slow moving and remained more or less coiled. They reacted to bright light and showed rapid undulating movement of the body. The nematodes were easily killed when immersed in water for a day or two or when kept in dry vials.

#### DISCUSSION

Determination of mermithid species is a very difficult task since usually only larval forms are available and these do not possess obvious morphological characters. A correct identification of the larva is only possible if it can be reared to the adult stage. Such rearing experiments have been accomplished only exceptionally by Christie (1937). Dr. H. E. Welch kindly provided continuous help in the matters of identification and according to him the nematode specimens obtained from the larval *Chrysops furcata* belong to the genus *Bathymermis*.

Concerning the biological control of tabanids only a few works have so far reported. Parman (1928) as quoted by Tashiro and Schwardt (1953) claims to have reduced viable tabanid eggs by 50% or more through the use of *Phanurus* (now *Telemonus*) *emersoni*, a hymenopterous parasite in parts of southwest Texas. James (1951) reported that *Diglochis occidentalis* a chalcidoid parasite, was an important agent in the natural regulation of the populations of larval tabanids in northern Manitoba. The results of the present report show a significant role of *Bathymermis* sp., in producing mortality among larval tabanids. The limited data available also suggest that transmission to other related larval host species is possible.

Further experimental work seems desirable to determine the specific nature of the life-cycle, to identify the parasite to the species level, to provide means for maintaining stocks and to ascertain the possible usefulness of the nematode in the biological control of larval tabanids.

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#### Book review

WIGGLESWORTH, Sir Vincent B. 1965. The Principles of Insect Physiology. 6th Edition. Methuen, London. vii + 741 pp. 407 figs. 4639 citations. 84 shillings.

The appearance of each new edition of Wigglesworth's *Principles of Insect Physiology* serves to quieten the consciences of most of us of lesser stature who have failed to keep up with the literature since its predecessor. This one is no exception. New citations, many referring to several papers, are given new alphabetical sequences, but numbered serially, as Supplementary References B at the end of each chapter. The substitution of a brief statement of the content in English for the original title is continued. This can be a bibliographical nuisance but is perhaps a valid comment on the titling of papers by insect physiologists. The indexes of authors have been consolidated. The fifteen chapter headings are unchanged in wording or sequence. The broad and lucid interpretation of physiology of the earlier editions is maintained and it is an eloquent testimony to the quality of these that changes, by and large, are additions rather than alterations. It is significant too that all other books of this scope in this field have multiple authors and that eleven of us are writing this review. We record here some errors in the book and some comments on it more in the hope of facilitating another edition in the fulness of time than of denigrating this one.

Although Wigglesworth rarely allows recent derivative work to overshadow that from which it stems, the omission of references for many early publications (e.g. Leuckart (1855) p. 2; Malpighi (1669) p. 317) is unfortunate; most of us have been conditioned to expect a reference when a name is followed by a date in parentheses.

The 1557 new citations contrast with the 234 which were added in the 1953 edition. The greatest proportional increase in number of citations is to be found in the chapters on nerve physiology, and especially chapter IV on the muscular system and locomotion in which there are nearly twice as many as in the fifth edition. The smallest increases are in the chapters on excretion and especially respiration in which there is only a 22% increase. The overall increase is more than 50%, as against less than 8% in the fifth edition. All of this is in keeping with our imp-

ression of the distribution of emphasis in research and the increasing pace of this.

In chapter III on growth the enormous accumulations of new material on hormones and diapause have been condensed into a masterful summary in which many of the "doubts and difficulties" referred to in the 5th edition have been laid to rest. Chapter IV contains a very much improved treatment of the action of indirect flight muscles in insects with high wing beat frequencies. No mention is made of the additional structural proteins of muscle, paramyosin and tropomyosin. In the discussion of locomotion on the surface of water (p. 143) volume and mass are treated as alternatives; both volume and mass of course vary as the cube of radius. More importantly, surface tension forces depend on the linear dimensions of the surface acting, not the area, so that the advantages of small size in this context are greater than indicated. *Tonofibrillae* is printed as two words on p. 133; *Sotavalta* is misspelled on p. 152 and again in the index of authors on p. 704.

Part of the increase in chapter V on the nervous system comes from two new sections, one on histology and histochemistry and the other on nutrition and ionic regulation in ganglia. There are several new illustrations. While neuromuscular transmission is appropriately discussed in chapter IV, the inclusion of much material on responses and muscle control in chapter V seems to call for a reference back to this.

Chapters VI and VII integrate much recent work on sense organs into an encouragingly traditional account of these structures. Since the dioptric part of the compound eye is far from cylindrical and the image formed by it "has no physiological significance" we think the treatment of image formation by a lens cylinder could be omitted, despite its bearing on apposition - superposition vision. While it is true that as stated on p. 212 the location and nature of the analyser (of the plane of polarization) have not been *fully* determined, this statement seems to contradict that on p. 213 "The analyser for polarized light is clearly in the rhabdomeres". In most places wavelengths have been correctly given in  $m\mu$ , a  $\mu\mu$  still appears on p. 215; on p. 192 (l. 22) for 'on an element' read 'as an element'. The inclusion of other senses in chapter VII might well be noted in the chapter title. Material on hearing in mosquitoes and bat avoiding by moths has been added. There is no mention of theories of olfactory perception, although many publications on these have appeared since 1953; perhaps if nothing good can be said, this is just as well. In chapter VIII on behaviour the outstanding additions are those dealing with communication including pheromones, and rhythmic behaviour and other rhythmic activities.

In chapters IX and X dealing with respiration and the vascular system there is no mention of the important work of Nunome. On p. 326 *Rhodnius* 253 should read *Rhodnius* 252. The work of Thorpe and Crisp (1949) appears in the original list of references (175) and also in the supplementary list (224). The simplification of the classification of haemocytes is to be welcomed.

The additional material on nutrition and digestion (chapter XI) represents supplementary detail rather than major advances, mostly dealing with enzyme secretion, enzyme action, and essential dietary components.



In chapter XII on excretion the work of Schindler (1878) on the surface area of Malpighian tubules has been misinterpreted (p. 505); a comma used for a decimal point in the original German has been read as a "thousands" comma, so that the areas are a thousand times greater than Schindler gives. Schindler's figures however are low since they assume the tubules to be right circular cylinders, whereas they are sinuous, and of course he was unaware of the microvilli. Allowing for these two points increases the area by a factor of about 70, so that Wigglesworth's figures remain high by a factor of about 14. It is remarkable that this mistake should have survived all previous editions, and no less remarkable that it was noticed independently by us and by A. Baynes of Trinity Hall, Cambridge, within a short time of each other, too late unfortunately for correction in the 6th edition.

In chapter XIII on metabolism there is further material on pheromones, an unfortunate, but perhaps unavoidable separation from that under behaviour. The glycolytic pathway is not given under respiratory metabolism, and again a reference back to the chapter on respiration would be helpful. In the discussion of the "surface law" (p. 568) it is said that there is no known reason why the metabolism of cold blooded animals should bear a relation to the body surface, but surely a tendency in this direction is to be expected where respiration depends on diffusion since this proceeds at a rate dependent on surface area. The references given under citation 345 are repeated under 479.

There is a relatively small increase in the content of chapter XIV on water and temperature, in which a somewhat conservative position is taken on, for example, the question of critical temperatures for water loss. Again cross references to other aspects of water balance, especially the integument, rectal glands, and Malpighian tubules would be useful; Beament's work for instance, is unmentioned in this chapter.

The final chapter, on reproduction contains added material on yolk formation, and RNA, DNA and protein synthesis. Woyke's work on diploid drone honey bees is not mentioned; perhaps this was too recent for inclusion.

This is a book which it is a pleasure to review. The binding and format remain unchanged, but the dust jacket in three colours illustrating the musculature of the crop of *Calliphora* and an aspect of the behaviour of *Eristalis*, is an innovation. Those parts of the content which are not already traditional will undoubtedly become so, and it is a final pleasure to record a traditional price.

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Publication of *Questiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

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TERRY L. ERWIN

# Quaestiones entomologicae



A periodical record of entomological investigations,  
published at the Department of Entomology, Uni-  
versity of Alberta, Edmonton, Canada.





## QUAESTIONES ENTOMOLOGICAE

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### LABRAL AND CIBARIAL SENSE ORGANS OF SOME MOSQUITOES

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*Quaestiones Entomologicae*  
2 : 259 - 270 1966

Sense organs on the labrum and in the cibarial pump of males and females of 22 species representing 8 genera of mosquitoes were investigated. Two types of sense organ were found on the labra of female mosquitoes, four hair sensilla at the tip and two subapical sensilla. The males of all species and the females of the non blood-sucking species *Toxorhynchites splendens* lack the four sensilla at the tip. The labral sense organs are innervated by a branch of the labral nerve. The cibarial sense organs are also found in two groups. A dorsal group of four types of sensillum on and around the anterior hard palate is indirectly innervated by a second branch of the labral nerve. A ventral group at the posterior end of the cibarial pump appears to be innervated only by a small branch of the fronto-labral nerve. A suggestion concerning the neuro-muscular mechanisms of the food path and their control of the passage of food is offered.

### INTRODUCTION

In 1921 Vogel published a study of the mouth parts of Culicidae and Tabanidae. The mosquitoes that Vogel used were *Culex pipiens* L., *Anopheles maculipennis* Meigen, and *Anopheles claviger* (Meigen). In his summary he states (our translation):

"In the ventrolateral edges of the labrum on each side there is a chitin canal which contains a protoplasmic thread and which is to be interpreted as a nerve. This thread or nerve ends in the labrum tip in a cell group which is located at the base of the fine chitin spines. The assumption that these are sense organs and apparently taste receptors is so much more probable since the other five stylets are completely chitinized at the tip."

In his text he also mentioned the number of observed spines:

"Anterior to the cell group the labrum ends in two tips formed from

the labrum canals, each of which has two chitin spines laterally . . ." Unfortunately Vogel's figures show only the cross-section of the labrum tip and therefore do not indicate the exact location of the sensory spines.

Robinson (1939) also described sense organs on the labrum of mosquitoes. He worked with the female of *Anopheles maculipennis*. Robinson referred to Vogel's work but may have misinterpreted it since his description differs from the original:

"At the tip, the stylet (labrum) is sharpened off ventrally like a quill pen and consequently the groove is open. Just below the point there is a pair of small pegs which may function as sense organs." and,

"In a transverse section of the labrum the internal (haemocoelar) lumen can be seen to be occupied by a pair of protoplasmic strands lying laterally. Vogel (1920) interprets these as nerves which terminate distally in sense organs in the position of small pegs." Robinson also referred to MacGregor (1931) who recorded:

"... the ability of *Aedes* and *Culex* to select a desired liquid by means of a sense located at the tip of the labrum."

Comparing Vogel's and Robinson's descriptions and illustrations, it becomes quite apparent that the two authors were describing two different sets of sense organs. Our study confirmed this.

Waldbauer (1962) examined the mouth parts of *Psorophora ciliata* (Fabricius), a culicid mosquito, under oil immersion. He did not record sense organs on the labrum, although the outer margins of apical setiform organs are shown in his fig. 17.

Snodgrass (1944) made a comprehensive study of the feeding apparatus of various groups of sucking insects and of generalized biting mouthparts. Unfortunately, although he referred to Vogel's and Robinson's work, he mentioned neither author in relation to taste receptors on the labrum. Snodgrass appears to have thought very little of sensory influence upon movements of the fascicle:

"Apparently however, the fascicle movements are entirely fortuitous, there being no evidence of a sensory influence, the fascicle often going close to a capillary without entering it, or sometimes penetrating clear through a blood vessel."

Snodgrass also mentioned MacGregor's work, but only in relation to the passage of food into the stomach or diverticula.

Day (1954) mentioned dorsal and palatal papillar sense organs in the cibarial pump. These had been described by Sinton and Covell (1927) and Barraud and Covell (1927) for their taxonomic value. Day described these sense organs in form and location and worked out some of the innervation. He believed that the sense organs are at least partially innervated by the frontal ganglion. Unfortunately, Day did not find any sense organs on the labra of his specimens. Day experimented with both males and females of *Aedes aegypti* L. He discovered that in males as well as in females blood was directed to the midgut, while sugar went to the diverticulum, although males do not usually imbibe blood.

Hosoi (1954) also worked on the food distribution mechanism in mosquitoes. He experimented with food stimulation of the entire fascicle and the labium and found that the fascicle is sensitive to whole blood and

to the corpuscles separately. He also found that the partial amputation of the fascicle reduced its sensitivity to food stimuli considerably, but that the mosquito was still quite capable of imbibing food especially if the proboscis stump were pushed into it:

"It is highly probable, therefore, that the sensory function of the fascicle originates in the labrum. It may be questioned, however, whether the receptors are located only on the tip of this organ, since mosquitoes imbibed blood into the stomach after the apical part of the fascicle had been amputated."

Hosoi suggested that the labrum should be sensitive along its entire length, and that food other than blood should also stimulate the labrum to some extent.

Christophers (1960) gave an excellent account of the fronto-labral nerve complex. He also described the gustatory papillae (see Robinson) on the labrum and both sensory groups of the cibarial pump. He did not however give the innervation of any of the sensory organs on the labrum or in the cibarial pump. Christophers was the first to mention that there are gustatory papillae on the labrum in both males and females. He also said that the cibarial sense organs are essentially the same in males and females.

Clements (1936) illustrated the labrum after Snodgrass but added sensory pegs (apparently taken from Robinson) without mentioning the change, despite the fact that Snodgrass found no sensory organs on the fascicle. He drew the subapical sensilla disproportionately large and omitted the apical bristle sensilla. Clements referred to Hosoi's work stating that the sense organs on the labrum and in the cibarial pump are at most only slightly sensitive to glucose, while they are sensitive to blood. Clements also took as fact assumptions made by Christophers and Day. Hosoi speculated that the labrum is sensitive over its entire length, but he did not work with this organ by itself. Furthermore, he made no reference to the cibarium or its sense organs.

Owen (1963) concluded that the fascicle of *Culiseta inornata* (Williston) bears no contact chemoreceptors. His statement is based upon experiments with feeding reactions of living mosquitoes after certain sensilla on the labium and tarsi were stimulated.

## MATERIALS AND METHODS

For the study of the labral sense organs the species listed in table 1 were used. Males and females were compared whenever possible. The least number of specimens used to represent one sex of one species was three. Whole mounts of both unstained and stained labra were used; the stains were vital methylene blue and crystal violet. The mounting media were DePex or Farrant's medium and both conventional and phase microscopy were employed.

The cibarial pump sense organs were studied by two methods. Whole mounts were made of the cibarial and pharyngeal pumps of all the specimens used for the labral study. The whole head was treated in KOH and dissected before mounting. The location and shape of the cibarial



sense organs could thus be determined.

Sectioned material was used to trace the innervation of the cibarial pump and the labrum. Males, females, and some pupae of *Aedes aegypti* were fixed in Masson's modification of Bouin's, washed and dehydrated via Zircle series, and embedded in Paraplast. Sections were cut at 3, 5, 7, and 10  $\mu$ . The stains used were Heidenhain's haematoxylin, aldehyde fuchsin, urea silver nitrate, and Novelli's nerve stain.

## OBSERVATIONS

The labrum is the thickest and stiffest of the six stylets forming the fascicle. It forms a double walled, ventrally closed tube, the food channel. The dorsal surface of the labrum is attached to the clypeus at the base, where the lateral edges of the inner wall widen out and are continuous with the roof of the cibarial pump. The hypopharynx forming the closure of the food channel at this point is attached to the membranous floor of the cibarial pump. At the tip, the labrum is slightly curved and cut off, as Robinson (1939) says, like a quill pen.

The cibarial pump is tubular and flattened dorso-ventrally. It extends from the base of the proboscis to just beyond the posterior edge of the clypeus where it ends in two lateral processes or flanges. Between these it is linked to the pharyngeal pump by membranes. The division between the cibarium and pharynx is marked by the insertion of two pre-cerebral dilators of the pharynx. These muscles lie between the frontal ganglion and the brain (Snodgrass 1944). The cibarial pump is mainly membranous but contains heavily sclerotized parts, the anterior hard palate, the posterior palate and the posterior sclerotized constriction which widens out into the lateral flanges. The two hard palates are dorsal, while the constriction is both ventral and dorsal. The pharyngeal dilator muscle inserts on the membrane just behind the constricted region of the cibarial pump.

### Labral Receptors

In the generalized female mosquito, ventrolaterally, in the lumen of the labrum, there are two canals (Vogel's chitin canals) which contain cytoplasmic strands. Each of these strands ends in a small group of cells near the tip of the labrum. There are no other cells in the labral canals. At the point where the food channel opens completely, each canal bears one sensillum. In most specimens this sensillum is round or slightly oval, has a heavily sclerotized rim and is usually covered by a thin membrane. In surface view, it looks like a campaniform sensillum. The diameter varies from 3 $\mu$  to 6 $\mu$  according to species in both males and females. Very fine dendrites lead from the group of cells in the canal to the sensillum. However, some specimens of certain species have a short peg projecting from the center of the membrane. When pegs are present these organs resemble minute basiconic sensilla surrounded by a wide membranous socket, figs. 3-8. The diameter of the membranous area is at least three times the diameter of the peg. Table 1 shows the species in which these basiconic-like sensilla were occasionally found.

TABLE 1. Sensilla on the labra of mosquitoes.

Species studied	Female		Male	
	Apical setiform	Peg in subapical*	Apical setiform	Peg in subapical*
<i>Aedes aegypti</i> (L.)	+	-	-	-
<i>albonotatus</i> (Coquillett)	+	-	-	-
<i>dorsalis</i> (Meigen)	+	+	-	-
<i>excrucians</i> (Walker)	+	-	-	-
<i>fitchii</i> (Felt & Young)	+	+	-	-
<i>flavescens</i> (Muller)	+	-	-	-
<i>spencerii</i> (Theobald)	+	+	-	-
<i>trichurus</i> (Dyar)	+	-	-	-
<i>vexans</i> (Meigen)	+	-	-	-
<i>Armigeres subalbatus</i> (Coquillett)	+	-	-	-
<i>Anopheles earlei</i> Vargas	+	-	-	-
<i>gambiae</i> Giles	+	-	-	-
<i>Culex fuscanus</i> Wiedemann	+	+	-	+
<i>pipens fatigans</i> Wiedemann	+	+	-	+
<i>pipiens pipiens</i> Linnaeus	+	+	-	+
<i>pipiens molestus</i> Forskal	+	-	-	-
<i>tarsalis</i> Coquillett	+	-	-	+
<i>territans</i> Walker	+	+	-	-
<i>Culiseta alaskaensis</i> (Ludlow)	+	+	-	-
<i>inornata</i> (Williston)	+	+	-	-
<i>morsitans</i> (Theobald)	+		-	-
<i>Mansonia perturbans</i> (Walker)	+	+	-	+
<i>Toxorhynchites splendens</i> (Wiedemann)	-	+ **	-	?
<i>Wyeomyia smithii</i> (Coquillett)	+	+	-	+

+ present, - absent

\* Socket-like subapical  
sensilla are present  
throughout.

\*\* See text, p. 264

Beyond the subapical sensilla, the labrum quickly assumes the form of an I in cross-section, and finally draws out into a fine point above each canal. At the extreme tip, each side bears two fine bristle or setiform sensilla (Vogel's chitin spines), fig. 3. The distal spines vary in length from  $9\mu$  in *Culex territans* to  $25\mu$  in *Aedes excrucians*, *A. fitchii*, and *A. flavescens*. The proximal and lateral pair may be either longer or shorter than the distal and medial pair, and varies from  $9\mu$  in *C. territans* to  $27\mu$  in the larger *Aedes* species. These bristles are set into membranous bases surrounded by heavy chitinous rings. They are hollow, and fine dendrites from the cell groups innervate them.

Whole mounts stained with vital methylene blue show the cytoplasmic strands and nuclei of the cell groups stained, thus suggesting nervous tissue. This assumption finds further support in serial sections stained with Heidenhain's haematoxylin, aldehyde fuchsin, or urea silver nitrate, which revealed nerves at the base of the labrum. Vogel (1921), Robinson (1939), Christophers (1960), and Clements (1963) assume also that the cytoplasmic strand should be considered a nerve.

The genera and species investigated differ little except in the size of the sensilla and in that the distance between the subapical and the setiform sensilla in *Culex* is relatively much longer than in the other genera, fig. 6.

One representative of the non blood-sucking genus *Toxorhynchites* Theobald was examined. The female of *T. splendens* (Wiedemann) has no apical setiform sensilla on the labrum. Subapical sensilla are present, and the labrum of *T. splendens* female (fig. 5) resembles the labra of males of other genera. The labrum of the male *T. splendens* differs a little in shape from that of the female, but bears only subapical sensilla as in males of other genera. Hairs project forwards from the membranous sockets of the subapical sensilla in both sexes and in this respect the subapical sensilla differ from those found in other genera, table 1. Two other autogenous species were examined *Wyeomyia smithii* (Coquillett) and *Aedes albopictus* (Coquillett). The labra of both species were normal; the females having four well developed apical sensilla. Other members of the genera *Wyeomyia* and *Aedes* are blood-suckers and the blood-feeding habit may be recently lost in autogenous species.

The labra of both sexes terminate in two pronounced chitinous points which are obscured in most females by the apical sensilla. The membrane between these points may be drawn out into a third point; this is especially pronounced in *Anopheles earlei* Vargas.

The labra of all the male mosquitoes studied lacked the apical setiform sensilla, figs. 7 and 8. Subapical sensilla were present and basiconic projections could be seen in some species (table 1).

#### Cibarial Receptors

There are two groups of sense organs in the cibarial pump, a dorsal and ventral group (figs. 1 and 9). The dorsal group is situated at the anterior end of the cibarium on and around the anterior hard palate, and consists of four types (Day's terminology):

Palatal papillar - Two pairs. Heavy spines with membranous bases.

Campaniform sensilla - one pair. Heavily sclerotized rings around membranous bases.

Dorsal papillar - one pair. Heavy spines. Base as in the campaniform but otherwise very similar to the palatal papillar.

Hair-like sensilla - number variable but usually three pairs. Base as in the campaniform sensilla but the ring is much smaller. The ventral group is situated at the extreme posterior part of the cibarial pump, usually in the heavily sclerotized neck region. The sensilla are of the short spine type and occur in two closely associated pairs, one pair on each side of the median line.

All sensilla in the cibarial pump are hollow and are innervated by fine dendrites originating from the sensory cells closely associated with them. Dendrites from the dorsal group lead to a larger group of loosely associated cells. This group lies dorsally to the cibarial pump and ventral to the retractors of the labrum, fig. 2. These muscles are innervated by the frontal nerve. The frontal ganglion lies dorsal to the junction between the cibarial and pharyngeal pump, and between the muscles leading to both these pumps. The frontal ganglion receives a branch of the fronto-labral nerve. This nerve arises on each side from the commissure and the suboesophageal ganglion. The nerve may branch immediately after leaving the commissure, but more often runs forward a little way before branching. The frontal ganglion connective passes dorsally anteriorly to the lateral flange of the cibarial pump to join the side of the frontal ganglion. The recurrent nerve issues from the posterior part of the frontal ganglion and runs just dorsal of the pharyngeal and suboesophageal pumps toward the neck region. The labral nerve branches soon after leaving the fronto-labral nerve. One branch (labral nerve I) passes forward and dorsally into the anterior and lower part of the clypeal dome, and splits up into fine neurons which supply the muscles and also the group of loosely associated cells previously described. The second branch (labral nerve II) passes forward along the side of and somewhat ventral to the cibarial pump and leads into the base of the labrum and into the labral canals (see fig. 2). In the generalized insect the labral nerve receives motor fibres from the frontal ganglion. We were unable to trace axons leading from the frontal ganglion to the labral nerve in any mosquito. It is quite plausible that axons lead directly from the sense organs to the tritocerebrum.

The ventral group of sensilla appears to be innervated by a small branch leading from the fronto-labral nerve to sensory cells associated with the sensilla.

The sense organs in the cibarial pump of male and female mosquitoes vary slightly in location, but no more than between specimens of the same sex and species. The general pattern does differ somewhat between different species and genera.

#### DISCUSSION AND CONCLUSION

The two types of labral sense organ described by Vogel and Robinson are both present. The apical bristles of Vogel have been overlooked



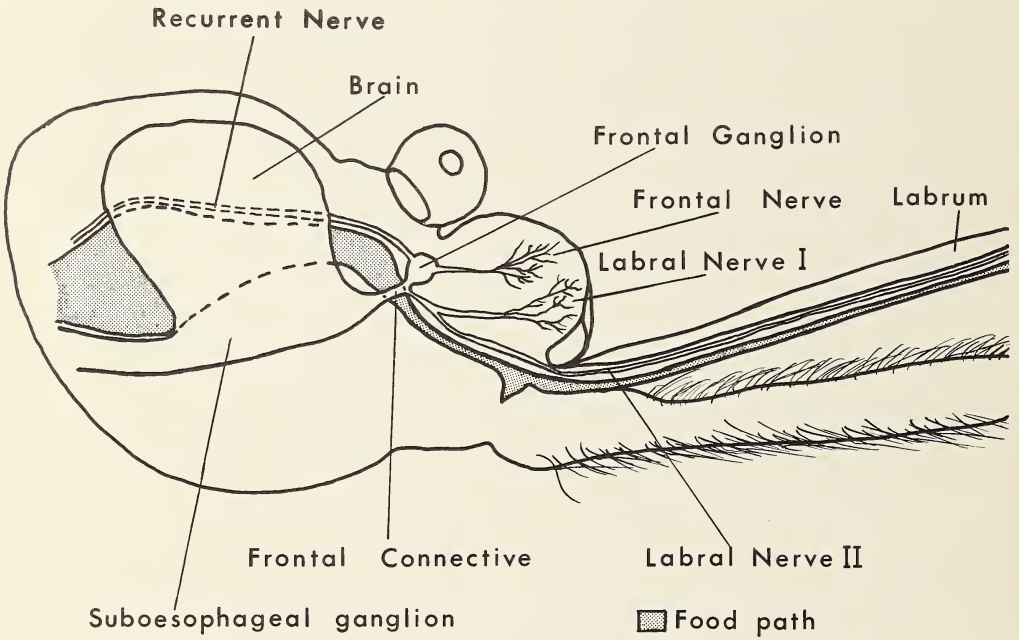
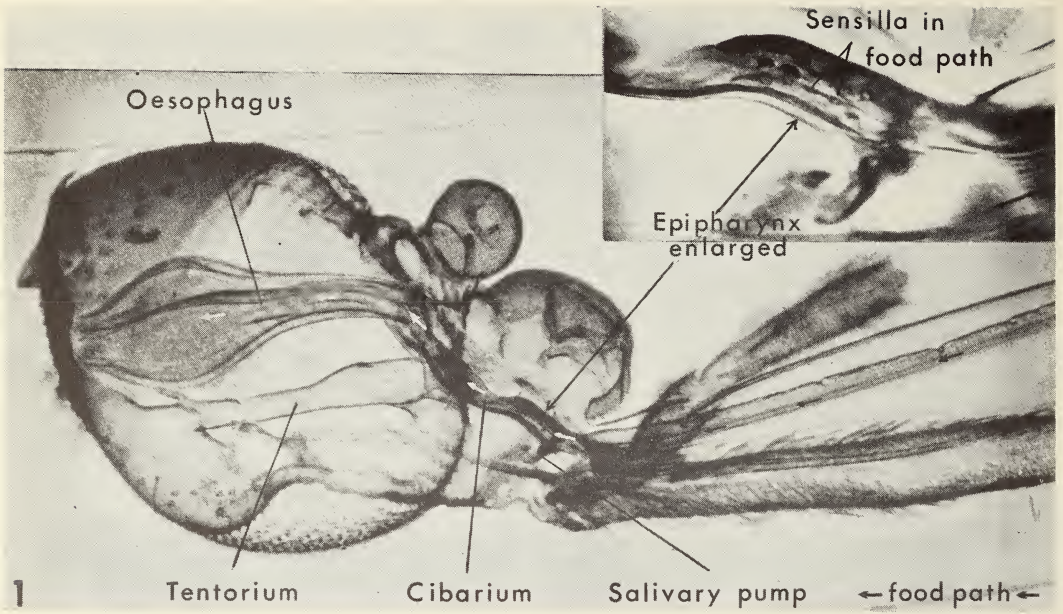


Fig. 1. Cuticular structures in the head of *Culiseta inornata* X 118; cleared in 5% KOH, right side removed.

Fig. 2. Outline of head and food channel showing the fronto-labral nerve complex. *Culiseta inornata* X 118.



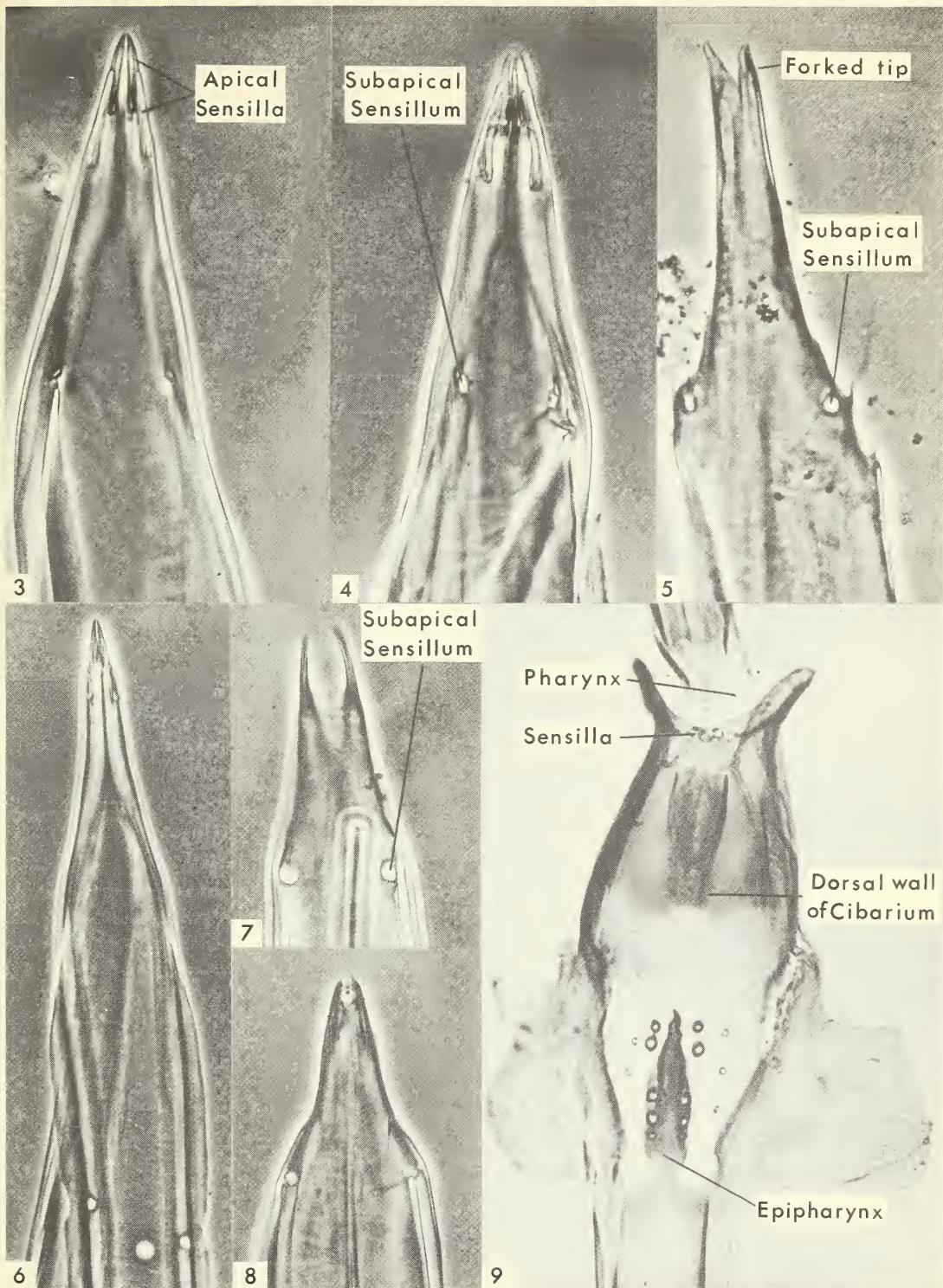


Fig. 3. Labrum of *Aedes vexans* ♀, X 590. Fig. 4. Labrum of *Aedes spencerii* ♀, X 590. Fig. 5. Labrum of *Toxorhynchites splendens* ♀, X 880. Fig. 6. Labrum of *Culex tarsalis* ♀, X 590. Fig. 7. Labrum of *Culiseta inornata* ♂, X 590. Fig. 8. Labrum of *Aedes vexans* ♂, X 590. Fig. 9. Dorsal wall of the cibarium of *Culiseta inornata*, X 265.

by recent workers because of their small size. Some species may lack Robinson's pegs, when only the thin socket is present. Both types are found on the labrum of female mosquitoes with the exception of *T. splendens*. They are indirectly innervated by one branch of the labral nerve and directly innervated by neurons leading from groups of sensory cells which lie in the anterior part of the labral canals. There are cytoplasmic strands but no other cells in the remaining length of the labral canals.

The cibarial pump sensilla are indirectly innervated by branches of the fronto-labral nerves. They are directly innervated by neurons leading from sensory cells closely associated with the sense organs and by those leading to a larger group of loosely associated cells just dorsal to the anterior end of the cibarial pump. The frontal ganglion appears to innervate only the various muscles of the pumps but may also innervate the large group of cells previously described. The ventral group of sensilla appears to be innervated only by a small branch of the fronto-labral nerve. Wenk (1953), in his paper describing the head of *Ctenocephalus canis*, describes a similar innervation of the cibarium and labrum. Day said that the cibarial sense organs are at least partially innervated by the frontal ganglion, but he was not able to trace the innervation with certainty.

Since the female labrum not only functions as a food channel but also in penetration and blood detection (Hosoi 1954) one would expect to find both mechano and chemoreceptors on the tip of the labrum. There are two types of sense organs present. Their functions could not be tested directly because of their very small size and close proximity. The apical setiform sensilla are hollow and innervated. One would not expect tactile hairs of this minute size to be hollow; also they are partially protected by the chitinous labrum tip (see Vogel 1921). They were never observed displaced and are therefore probably chemoreceptors rather than mechanoreceptors.

The male labrum has only the subapical sensilla; setiform sensilla are never present. The male normally feeds on exposed sugary fluids and does not have to pierce any tissue when feeding on nectar, but will penetrate fruit when kept in the laboratory. As the labrum of both sexes is only very slightly sensitive to sugar (Hosoi 1954), the subapical sensilla on the labra of males are unlikely to be chemoreceptors. The apical setiform sensilla in the female are most likely to be chemoreceptors which function in detection of blood or some component of it. This idea is supported by the fact that the female *T. splendens* which does not feed on blood lacks the apical setiform sensilla.

The subapical sensilla may be mechanoreceptors; in all except the genus *Culex* they are positioned at the end of the stiff side channels where campaniform sensilla could detect the bending of the tip. However they may be placoid or small basiconic chemoreceptors. Further behavioral studies involving micromanipulation and electron microscope work are required to resolve this question.

No morphological support could be found for Hosoi's suggestion that the labrum might be sensitive along its entire length. On the contrary, it was found that the labrum is not permeable to crystal violet (Slifer 1960) except at its very tip, and there only slightly. Some sen-



sitivity of the lower part of the labrum would be expected after cutting off the tip and thus exposing the nerves in the labral canals. It is probable that food is detected by the apical labral sense organs and the pumping action is initiated by impulses received by the cibarial muscles from the labral sense organs via the frontal ganglion. A preliminary distinction between blood and sugar solutions may be made by the labrum. After the food enters the cibarial pump, the various sensilla there are excited and send out impulses to the muscles controlling the openings of the stomach and diverticula, thus setting the food-directing mechanism in action. This would explain Hosoi's finding that blood is sent into the stomach and sugar solutions into the diverticula even after the fascicle had been cut off. Further investigation is required to verify this.

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## BEHAVIOUR OF LARVAL TABANIDS (DIPTERA : TABANIDAE) IN RELATION TO LIGHT, MOISTURE, AND TEMPERATURE

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The behaviour of larval *Tabanus reinwardtii* Wied., *Chrysops furcata* Walk., and *Chrysops mitis* O. S., in relation to light, moisture and temperature was studied. Rate of movement, aggregation, and localized movements of the head capsule were used as criteria for analyzing larval behaviour. The anterior region of the larval head capsule is sensitive to light; a pair of eye spots on the head capsule is suggested as the photoreceptors. On illumination larvae are able to integrate light energy over periods of seconds and to utilize this to produce a directional response. Larval *C. furcata* and *C. mitis* show no preference for the dry or the wet side in various humidity gradients. However, they show abnormal behaviour on a uniformly dry substratum. The mean water content of *C. mitis* larvae is 79.5% and the effects of desiccation on survival are discussed. The reactions of *C. furcata* and *C. mitis* larvae in uniform temperatures and in temperature gradients are described. The speed of movement and time percentage of activity, though affected by temperature, are shown to be more affected by light. 21.4–0.8°C is suggested as the 'preferred temperature' of larval *C. mitis*, 37 – 40°C is lethal to the larvae. Light and temperature are the most important environmental factors.

Cameron (1917) is the only investigator who has noted that larval tabanids, like other soil insects, are negatively phototactic. Other than this no work has been published on larval reactions to environmental factors. The chief aim of the present work has been to investigate the orienting reactions of larvae in relation to the light, moisture, and thermal stimuli the larvae encounter in their natural environment. An attempt has been made to relate the results of this laboratory study to the activities of larval tabanids under natural conditions.

**Collecting Methods**

Larvae were obtained from the mud of irrigation ditches, along the banks of streams, pools and swamps. The method recommended by Marchand (1920) of separating the larvae by washing the soil through a sieve was most effective in collection of *Chrysops mitis* O.S. and *Tabanus reinwardtii* Wied. but *Chrysops furcata* Walk. were obtained by turning over the soil with a garden fork. The first collection was made on October 7, 1958 at Winterburn swamp, 8 miles west of Edmonton. The vegetation consisted chiefly of sphagnum moss and sedges, marsh cinquefoil, spruce, larch, Canada blue grass and marsh reed grass. Larval *C. furcata* were collected on the west banks of the pools. Pupating larvae were found as a rule 1 - 2 inches below the surface at the pool's edge. Small larvae were found deeper in the soil and often submerged in water. The second collection site was a grassy lake near Raymond, about 18 miles south of Lethbridge, Alberta. This area consisted of about 200 acres of clay soil covered with a shallow layer of organic matter and interspersed

with slough grass (*Beckmannia* sp.). Larval *T. reinwardtii* were found at depths of 2 - 3 inches below the surface. Two roadside irrigation streams near Vauxhall and Waterton, Alberta, were most productive for larval *C. mitis*. The average depth of water in the middle of the stream was 2 - 3 feet. Larvae of various sizes were obtained from the mud entangled with heavy growth of algae (*Cladophora* sp.) and completely submerged in water. The vegetation bordering the stream banks was sparse. Only the Raymond soil where larval *T. reinwardtii* were found, was acidic. Organic matter content was high, an average of 69% for the Winterburn soil and 42.5% for Raymond, Vauxhall and Waterton soils.

#### Maintenance of Stocks

Larval stocks in the laboratory were maintained as recommended by Shemanchuk. Larvae were stored in 3 x 1 inch plastic vials with a soil medium rich in decaying organic matter. No other food was supplied. These larvae when kept at 5 - 10 C in a refrigerator, did not pupate. Room temperature of 21 C brought about pupation of mature larvae in a few days. The average pupal period determined from six specimens (5 female and 1 male) of *C. mitis* was 7 days. For *C. furcata* it was 11 days, based on 3 females and 7 males.

Larvae of *Tabanus* sp., occasionally struck each other when placed together in a dish. However, cannibalism was never observed. Larvae of *Chrysops* spp., showed less interest in fresh animal tissues even though they were kept together in vials with clean tap water and starved for a month or more. Greater activity amongst larval *C. mitis* than *C. furcata* was observed under laboratory conditions. Larval *T. reinwardtii* did not survive such long periods in water as the larvae of *Chrysops* spp.

Mortality during maintenance of larval stocks ranged up to 40% chiefly due to fungus growth, a nematode identified by Dr. H. E. Welch, Belleville, Ontario as *Bathymermis* sp. (Shamsuddin 1966) and inadequate ventilation. Few deaths occurred when the soil was changed once every 3 months and when the storage vials were provided with perforated caps to ensure proper ventilation.

#### BEHAVIOUR OF LARVAL TABANIDS IN RELATION TO LIGHT

The effect of light on the rate of locomotion of eyeless forms has been less studied than orientation to light. Welsh (1932, 1933), working with *Unionicola* (Arachnida), concluded that in a light sensitive organism the extent of muscular activity bears a definite relationship to the intensity of illumination. Duggar (1936), Jones (1955), and Millott (1957) give good summaries of photokinesis in eyeless forms of insects, echinoderms, and molluscs. Miller (1929) has discussed the results obtained by Mast (1911) and Herms (1911) on the speed of crawling of fly larvae (*Calliphora*, *Sarcophaga*, and *Musca* sp.).

Further information is included in the works of Holmes (1905), Patten (1914, 1915, 1916), Loeb (1918), Crozier (1927), Mitchell and Crozier (1928), Ellsworth (1933), Fraenkel and Gunn (1940), Bolwig (1946), and Hafez (1950, 1953) on the photonegative responses of muscoid

larvae. There is a general agreement that fly larvae behave photonegatively and that their mechanism of orientation to light represents typical klinotaxis (Carthy 1958). However, a wide diversity of opinion prevailed for a long time as to the true nature of photoreceptors in fly larvae. Lowne (1890-95) as quoted by Hollaender (1956) described two pairs of small papillae on the apex of the larval head as being photosensitive. Ellsworth (1933), on the basis of histological findings in *Lucilia* sp., reported the presence of photoreceptors on the larval maxillary lobes. However, Welsh (1937) indicated that the sensory papillae of fly maggots previously regarded as photoreceptors are gustatory. The photoreceptors of housefly larva were finally identified by Bolwig (1946) as two small groups of sense cells, situated one on each side just above the anterior ends of the larval pharyngeal sclerites.

Important information has been obtained on the photosensitive organs of the eyeless forms by using localized stimulation through light patches (Harper 1905, Herms 1914, Hess 1921, 1924, 1925, Ellsworth 1933, Young 1935, Hawes 1945, Newth and Ross 1955, Yoshida 1956, 1957, and Millott 1957). Such a method has also been used for investigation of dermal photosensitivity of forms ranging from invertebrates, through lower chordates to vertebrates. Localization of sensitivity is, however, too ill defined and an electrophysiological demonstration of photosensitivity is still needed.

#### Experimental Methods

Experiments were done from May 1, 1959 to January 4, 1960 in a dark room at a temperature of  $23.3 \pm 2.8$  C. Two glass plates, 35 x 70 cm and 45 x 60 cm and a photographic tray measuring 22 x 17 cm were used. In all experiments the plates rested on black paper. One of the light sources was a photographic enlarger with a 75 watt bulb. Low light intensities were obtained by using the enlarger lens which had a focal length of 150 mm. High light intensities were obtained from 100 - 150 watt electric bulbs enclosed in a light tight box. The difficulty of observing in the dark room was overcome by using a photographic safe light which, according to the manufacturers, transmitted wave lengths beyond 580 m $\mu$ .

Mature larvae of *Tabanus reinwardtii* and *Chrysops furcata* were kept in 3 x 1 inch plastic vials with about 1/2 inch of tap water and stored in the dark room. If the larvae were exposed to light in an experiment they were allowed at least 1/2 hour rest in the dark before being used in another experiment. Observations were usually made on single larvae. The glass was treated with a water suspension of talc on which the larva crawled leaving a trail behind it. During each experiment, time intervals were marked with a wax pencil. The tracks were measured with a map measurer.

#### Preliminary Studies

##### *Activity in the dark*

One hundred and eighteen larvae in separate glass vials containing either clean moist sand or tap water were watched under the red light singly for 3 minutes each. About 86% of the larvae showed activity char-



acterised by flexing of the body and occasional crawling. Such activities could be easily mistaken for responses to light stimulation. It was, therefore, necessary to record each type of activity for a small group of 20 larvae with the help of a hand lens. These larvae were placed on the tray under the red illumination. All of them crawled; however, a response characteristic of behaviour under the experimental white light i. e., withdrawal of the head capsule into the cephalic collar preparatory to crawling, was never shown. When 34 animals were put singly on the glass plate, each for 5 minutes, all responded by crawling. A mean speed of  $1.6 \pm 1.1$  cm/min was recorded for these larvae. This is taken as a basal rate of movement of larvae in the dark.

#### *Response to general illumination*

If the experimental white light was turned on when the larvae were inactive or crawling they hesitated momentarily, raised the anterior tip, swung it violently from side to side in an exploratory fashion and then withdrew the head capsule into the cephalic collar. The sudden withdrawal of the head capsule was found to be a reliable indicator for photic response and henceforth will be referred to as the 'retraction reflex'.

The 'retraction reflex' was usually followed by a further series of head movements, then by turning movements involving the whole body, finally by crawling. Hence there are measurable time intervals between the onset of illumination and the 'retraction reflex' and crawling. The first time interval is referred to as the 'reaction time' of larvae which is the period from the time of illumination until the head capsule is withdrawn. Preliminary experiments showed that illumination must be continuous during the reaction time. The 2nd time interval is the period elapsing from the end of the 'retraction reflex' until crawling is started and is referred to as the 'crawling time'.

#### **Reaction Time and Crawling Time**

The light sources used were the photographic enlarger and the electric bulbs as described earlier. To ensure that temperature did not affect the reaction time, glass heat filters were used in the intensity range of 100 - 1600 foot-candles. The experimental trough always contained at least 50 cc of tap water and a rectangular blotting paper matting 19 x 14 cm. A glass vial containing one *C. fuscata* larva with about 1 cm water was emptied over the tray and an interval of 1 minute was allowed. The light was then switched on and two stop watches started simultaneously. One of them was used to record the reaction time and the other the time to crawl.

The results obtained with 3 different groups of larvae are summarized in fig. 1. All larvae showed a great variation in reaction time even under the same light source and intensity. This was particularly true in the low light intensities. At high intensities the reaction time approaches a minimum and is little affected by great increases in intensity. The reaction time of each group varies inversely with the logarithm of the intensity.

The crawling time for a group of 5 larvae tested 10 times each is also given in fig. 1. Considerable variation was shown by individual

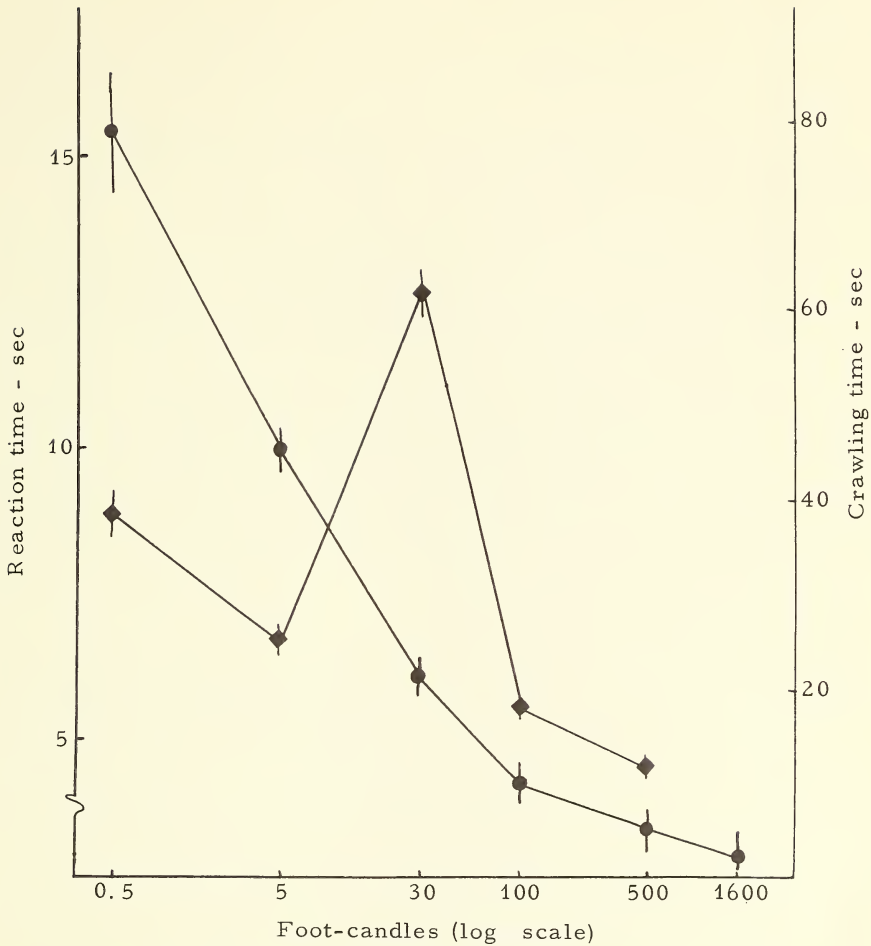


Fig. 1. The relation between reaction time (●155 readings with 70 larvae) and crawling time (◆50 readings with 5 larvae) and light intensity for *C. fuscata*. Lines indicate standard errors.

larvae. No relationship was found between the reaction time and the crawling time. For example, larvae with a short reaction time at a given intensity did not necessarily show a short crawling time. However, apart from the anomalous data at 30 foot-candles, crawling time decreases with increasing light intensity.

### Photoreceptive Organs

#### Structure

Preliminary experiments indicated that larval tabanids have a light sense located in the eye spots. Gross dissections, injection of vital stains, and serial sectioning all failed to reveal nerve connections to these although gross concentrations of pigment were found.

*Experimental*

A satisfactory method of obtaining local illumination was by replacing one ocular of a binocular microscope with a microscope lamp so that the rays converged through the objective. The diameter of the light spot could be changed from 0.8 to 12.0 mm by changing the microscope objectives. This arrangement provided a precise diameter of light spot.

Twenty mature larvae of *C. furcata* were chilled for one minute and examined with a 1 mm diameter pencil of light. Responses were obtained as follows: head capsule, 20; 3rd thoracic segment, 1; abdominal segments, none; Graber's organ and siphon, 5. This experiment demonstrated that the larvae have maximum sensitivity to light in the head region.

In another experiment 3 mature larvae of *T. reinwardtii* were kept in a light of 7 foot-candles for an hour before the light pencil test started. All parts of the body of each animal were carefully searched with the light pencil apparatus giving a light spot 2 mm in diameter. When the local light reached the pigmented spots described as eye spots in the larva of *Haematopota pluvialis* L. (Tabanidae) by Cameron in 1934, situated latero-dorsally on the head capsule, the larvae responded by turning away from the light source. Localization of the light pencil on the eye spots was a difficult task owing to the extreme mobility of the head capsule. However, whenever this was achieved, it caused violent head movements of the larva. This reaction was maximal when the head capsule remained projected out with the eye spots completely exposed.

Attempts to paint the eye spots with a mixture of India ink and gum arabic were not successful. It was, however, possible to paint the anterior head capsule including the eye spots of six larval *Chrysops*. Fig. 2 shows the area of the head which was painted. After blackening, the larvae were stored in the dark for an hour and then examined by local and general illumination. The response varied from none to incomplete withdrawal of the head capsule under local illumination with a 1 mm light spot. But under a 10 mm light spot, the reaction was obvious in all the larvae. When the painted areas were washed and the tests repeated the larvae displayed the typical 'retraction reflex'.

To see if the anterior tip of the head capsule was responsible for sensitivity to light as has been demonstrated in *Lucilia sericata* by Ellsworth (1933), 1 mm of the anterior head tips were cut off from each of 7 larvae. Ten such operations were done; 3 died immediately but the remaining 7 were in healthy conditions for several months. Reaction times for these were recorded one day after the operation, under both local and general illumination. The mean reaction time at 100 foot-candles was 28.7 sec, much higher than any of the values of fig. 1. Thus although the removal of the anterior tip does not alter the character of the 'retraction reflex', it does increase the reaction time considerably.

The results of these experiments demonstrate the presence of photosensitive organs in the head capsule. The experiments on painting indicate that dermal sensitivity also exists in larval tabanids. The considerable increase in reaction times on removal of the anterior tip suggests that photosensitivity is spread throughout the anterior region of the

head capsule. We cannot yet specify the nature of the photoreceptors in larval tabanids beyond stating that they appear to be contained in the anterior region of the head capsule, perhaps the eye spots.

#### Reactions in a Dark-Light Choice Chamber

Two petri dish lids with a diameter of 15 cm, were placed one upon the other with the edges in contact. A moistened disc of about 2 mm thick brown cardboard divided the chamber into an upper and lower half. The lower half of the chamber was filled with water which remained in contact with the cardboard partition throughout the experiments. For each experiment a separate card was used. This arrangement kept the cardboard surface, on which the animals crawled, moist. One half of the chamber was covered with black cardboard to provide a choice of dark and light. The light source was the photographic enlarger.

Fifty mature larval *C. furcata* were used. Ten larvae were put in the center of the choice chamber at a time and their positions were recorded after 15 minutes. The results are summarized in table 1. The intensity of light reaction is expressed as  $100 (D-L)/N$  (Perttunen 1959), where D represents the number of larvae on the dark side, L the number of larvae on the illuminated side and N the total number of position records.

TABLE 1. Intensity of light reaction of larval *Chrysops furcata* Walk. in a choice chamber of darkness and light; mean of 5 experiments with the same 50 specimens at each light intensity, temperature  $23.3 \pm 2.7^\circ \text{C}$ .

Light intensity in foot-candles	Mean intensity of reaction, $100 (D-L)/N$ after 15 min.	SD	SE
0.25	57.4	12.3	5.5
0.50	47.3	16.3	7.3
1.00	63.2	29.0	12.9
2.00	52.4	25.8	11.5
5.00	70.3	26.8	11.9
10.00	71.3	17.3	7.7

At room temperature the larvae of *C. furcata* behave photonegatively at all the intensities used. The intensity of reaction, however, does not show a regular increase with increase in light intensity.

#### Intensity of Illumination X Speed of Crawling

It was anticipated that larval tabanids may move at different speeds at different light intensities, for light frequently has an effect on the rate of movement of animals, including dipterous larvae (Fraenkel and Gunn 1940). A series of measurements was made with each of 7 - 10 larvae at each light intensity in the range of 0.03 - 500 foot-candles. Larvae were placed in the center of the glass plate. The light was switched on 30 seconds later. Each larva was allowed to crawl for 5 minutes, but





Fig. 2. Photomicrograph of the cephalic segments with the head capsule projected out, showing the area painted. Larva of *C. furcata* Walk.

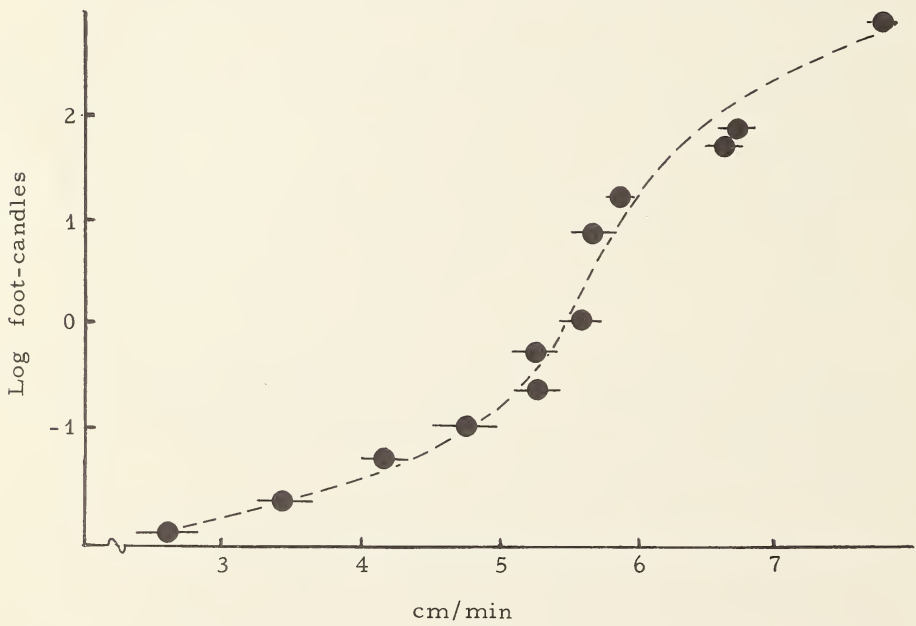


Fig. 3. Effect of light intensity on the speed of movement of larval *C. furcata*. Lines indicate standard errors.

only the track of the middle 3 minutes was measured. The average speed in cm/min was recorded. The results are summarised in fig. 3. The curve is sigmoid, but there is close agreement with the Weber-Fechner law (Patten 1915) in the range of 10 - 500 foot-candles.

#### **Behaviour in a Light-Gradient**

The construction of the light-gradient apparatus was fundamentally similar to the 'non-directional' gradient described by Ullyott (1936). A steep gradient was arranged with a glass diffusing plate and a more moderate gradient with a graded film in an enlarger. The former ranged from 150 to nearly zero foot-candles over 30 cm, the latter from about 50 foot-candles to zero over the same distance. Each gradient was oriented with the high intensity to the east.

A larva was placed in the center of the experimental plate with its head directed towards east. The experimental light was switched on after 30 seconds and the direction of movement in relation to the light-gradient was recorded at the end of 5 minutes. Fifty larvae were used in these experiments. The tracks of 18 other larvae were recorded by placing a single larva in any part of the experimental plate and leaving it for 3 minutes in the dark. The light was then switched on and the observations made till the larva reached the edge of the glass.

The results obtained with 50 larvae are shown in table 2. If movements were at random with respect to the light-gradients then we would expect to find a mean number of 6.25 larvae going in each of 8 directions. A chi-square test applying Yates' correction for small numbers was used for these data. The purpose was to assess the probability of any one direction being chosen by the larvae in the light-gradient. The chi-square value obtained for the moderate gradient is significant at the 2% level. It is, therefore, obvious that the larvae do not move in all directions in equal numbers. The chi-square value for the steep gradient is not significant at the 5% level. The greatest number of larvae, however, moved in the westerly direction, that is down the light intensity gradient.

Larvae which were placed in the gradients with their heads facing the high intensity zone showed turning movements towards the darker ends of either gradient. In fact, the longer time interval between the first illumination and crawling favoured the chance of a directed orientation in the low intensity region of the gradient.

#### **Lateral Light Stimulation**

##### *Reactions to two balanced lateral sources*

Loeb (1905) has pointed out that "when two sources of light of equal intensity and distance act simultaneously upon a (negatively) heliotropic animal, the animal puts its median plane at right angles to the line connecting the two sources of light". We should expect, then, that a larva, subjected to the action of opposed beams of equal intensity, would continue crawling in a direction at a right angle to a line connecting the two sources. That such is the case with blowfly larvae has been demonstrated by Patten (1915). Since larval tabanids in preliminary experiments showed a photonegative reaction in a horizontal beam of light, it was thought necessary to check their reaction under balanced illumination.

TABLE 2. The directions taken by 40 larval *Chrysops fuscata* Walk. at the end of 5 minutes in light-gradients. Each larva was placed at the center, 15 cm from the maximum intensity.

STEEP GRADIENT	Min. light				Max. light			
	W	NW	SW	N	S	NE	SE	E
Observed	12	9	5	5	3	6	5	5
Observed minus random (O-R)	+5.75	+2.25	-1.25	-1.25	-3.25	-0.25	-1.25	-1.25
	$\chi^2 = 9.52$							
MODERATE GRADIENT								
	W	NW	SW	N	S	NE	SE	E
Observed	15	8	3	5	4	6	5	4
Observed minus random (O-R)	+8.75	+1.75	-3.25	-1.25	-2.25	-0.25	-1.25	-2.25
	$\chi^2 = 17.12$							

Three 25 watt lamps in light proof cases with rectangular apertures 3 x 1 cm, cut in one face were used. The lights were placed in the centers of 3 sides of a 54 x 54 cm wooden board with the apertures facing the center. Fourteen larvae of *C. fuscata* were used. With the lights switched off each larva was put on the center of a 23 cm diameter glass plate so that the axis of its body was at right angles to the line joining the balanced lights with its head pointing away from the unbalanced light. The balanced lights were then switched on simultaneously, and the course of movement was recorded. The unbalanced light remained off in these experiments.

The average direction of several courses taken by each of the 14 larvae in 74 trails is represented in fig. 4. The general pattern in taking course 1 (straight ahead) was shown by about 67% of the larvae. The tendency to deviate from the expected course was more pronounced in the immature larvae. 8% of the larvae crawled to one or other of the

balanced lights.

*Reaction to a change of 90° in the direction of illumination*

The results described above suggests that (1) orientation of larval tabanids, as of blowfly larvae (Patten 1915, 1916) to balanced and opposed illumination depends upon symmetrically located bilateral sensitive areas; and that (2) such an orientation varies with the age of larvae. To further test these two points, the following experiments were conducted.

Preliminary experiments were done to select larvae of uniform sensitivity as described by Patten (1916). Nine mature and eight immature larval *C. furcata* which reacted by changing their course of movement with reference to an instantaneous change of 90° in the direction of a beam of light were selected and used in these experiments.

The arrangement of the lights was the same as before but the larvae were placed with heads pointing away from one of the balanced lights. The left or right balanced light was kept on until larvae reached close to the center of the circular glass plate. The direction of the incident light was then changed through 90° by switching on the unbalanced light instead. Each larva was allowed to crawl through twice, once under the influence of the left light and once under the influence of the right. The tracks were traced. The total change in direction of travel in 3 cm from the point at which the light was changed was measured as shown in fig. 5, by means of a protractor. Thus the average angular deflection of two trails was recorded as the response of a larva to the change of 90° in the direction of illumination.

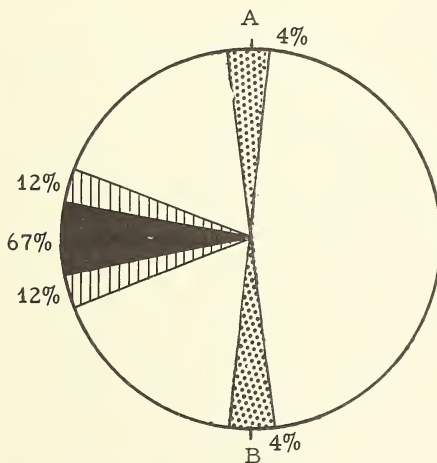


Fig. 4. The directions of movement of larvae in two beams of light from equal and opposite sources A and B.

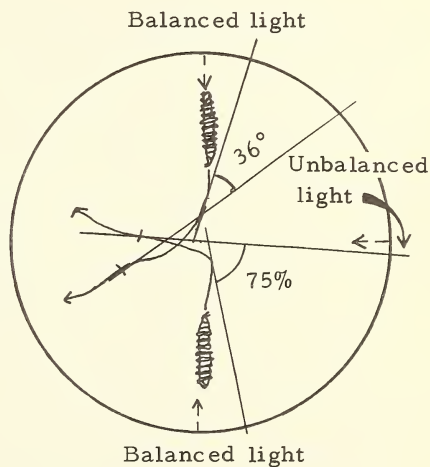


Fig. 5. Two trails of larva no. 9. The starting (balanced) light was switched off and the unbalanced light on when the animal reached close to the centre.



The results are shown in table 3. It can be seen that the change in the direction from which the lateral light acts causes corresponding changes in the direction of locomotion of the larva. However, such a change is subject to considerable variation. The average values of two trails range from 4.5 to 60° in the immature and 51.5 to 90° in the mature larvae, so that a more accurate orientation to the change of 90° in the direction of illumination is shown by mature larvae. It seems, therefore, that a large part of the variation in response to the lateral light stimulation is due to the difference in age of the larvae. Such a variation has been reported in larvae of several species of the family Caliphoridae (Patten 1916).

TABLE 3. The angular deflection measured in degrees of 17 larvae of *Chrysops turcata* Walk. subjected to a change of 90 degrees in the direction of light. Averages of a right and left pair of trails in fig. 5.

	1st trail Right	2nd trail Left	Average in degrees
Immature	5	4	4.5
	80	40	60.0
	8	45	26.5
	34	10	22.0
	75	36	55.0
	30	68	49.0
	55	29	42.0
	58	23	40.5
			Mean 37.4°
Mature	75	20	47.5
	82	45	63.5
	65	50	57.5
	58	110	84.0
	53	64	58.5
	100	56	78.0
	87	68	77.5
	90	91	90.5
	45	38	41.5
			Mean 66.5°

### Discussion

Larval *Chrysops* react to light in two different ways. One is by suddenly withdrawing the head capsule and the other by crawling. Reactions similar to the first response have been recorded in widely different forms of animals such as hydroid polyps, sea-anemones, tubicolous worms, several echinoderms and certain molluscs (Hollaender 1956) and are commonly known as the 'retraction reflex'.

The reaction times of 3 groups of larvae determined at different intensities formed a hyperbolic relationship when plotted against the

logarithm of light intensity (fig. 4). This is roughly in agreement with the Bunsen-Roscoe Law of reciprocity (Steven 1950). According to Adrian (1928) this law represents only the mid-region of an integral distribution curve which is expected from the addition of more and more active receptors with increasing intensity of stimulus. Pirenne (1956) reports increased variation in the photic response of various groups of organisms as the threshold is approached. The relatively large deviations from the theoretical line (fig. 3) in the low intensity region agree with these views. The deviations in the entire range may be due to an uncontrollable error, owing to a continuous change in the intensity of illumination of larval photoreceptors during movement. This can be easily brought about by the extension and retraction of the larval head capsule. Further, the works of Patten (1915), Hecht (1918), and Hartline and Graham (1932) point out that the Weber-Fechner law cannot describe responses in which several steps intervene between the stimulus and the response. Since locomotion in the larval tabanids represents a complex or integrated response which is brought about by two different reactions as shown earlier, the whole process cannot be properly described by this law.

In the choice chamber experiments, the larvae tended to aggregate around the wall of the chamber. The contact produced a slowing down of locomotion and also affected the direction of this. This means that although larval *Chrysops* are photonegative in the choice chamber, their behaviour to light is subject to interference by the uncontrollable factor of thigmotaxis. This may be why the intensity of reaction (table 1) in the choice chamber was not directly proportional to the logarithm of the light intensity.

The behaviour in dorsal light gradients suggests that larvae react orthokinetically in the higher intensity zone. But at lower intensities they seem to react klinotactically. Thus larvae left at the dark end of the gradient seldom moved up the gradient. They apparently showed directed reactions and turned back. It further seems that larvae arrive at the dark area as a result of 3 factors: (1) the 'retraction reflex'; (2) the local movement between the 'retraction reflex' and crawling; and (3) the increase in speed of locomotion due to an increase in light intensity. These observations and the data in table 2 suggest that the larval reactions were not truly random. Therefore the behaviour in a dorsal light gradient can be satisfactorily described in terms of a combination of orthokinesis and klinotaxis.

The experiments on lateral light stimulation show that larval tabanids, like *Musca*, *Calliphora*, and *Lucilia* larvae (Fraenkel and Gunn 1940), display a photonegative reaction in a horizontal beam of light. The orientation away from the light source is chiefly attained by klinotaxis.

These findings suggest that a negative phototaxis coupled with photo-orthokinesis fit the larva well for its environment. It will lie relatively inactive in the dark within the soil. If exposed, it will become active. The negative phototaxis would add an orienting factor making the return to soil more rapid. Light reactions can, therefore, explain the apparent absence of larvae from the surface of the soil. Changes in them with age may also explain why larvae are found in different situations as they mature.

## REACTIONS OF LARVAL TABANIDS TO MOISTURE

Although soil moisture is an important environmental factor, the influence of water as distinct from air humidity, on insect behaviour has not been widely investigated. Work on insect reactions to moisture has been reviewed by Lees (1943). Since then, practically no work has been published in this regard. Little is known about the humidity sense and orientation in semi-aquatic insects. The humidity and moisture reactions and data on water loss of the larvae of two species, *C. furcata* and *C. mitis* are reported here.

**Experimental Methods**

In most experiments the choice chamber method as described by Gunn and Kennedy (1936), Wigglesworth (1941), and Lees (1943) was used.

Three different types of humidity chambers were employed. Type 1 consisted of a cylindrical glass vessel, 15 cm in diameter and 6 cm deep. This was closed by a glass plate with a sealable hole, 3 cm in diameter in the middle. A vertical partition 2.5 cm deep was attached to the glass roof to divide the chamber into two halves. A petri dish, 14 cm in diameter, which was divided into two halves by a thin glass partition 2.5 cm deep formed the floor of the chamber. A false floor of wire gauze was supported from the actual floor. In a few experiments layers of glass beads (average diameter about 2 mm) were introduced on the wire gauze tray to facilitate the movement of the larvae. This was used as a constant humidity chamber by removing the partition from the glass roof and the petri dish. Type 2 consisted of two petri dish lids, 10 cm in diameter and 1 cm deep, placed one upon the other with their well-ground edges in contact. A disc of 1 mm mesh saran gauze divided the chamber into an upper and a lower half. Type 3 apparatus was essentially the same as in 2, except that the two lids had a diameter of 7.3 cm and were 0.7 cm deep and the lower lid was divided into two halves by a thin glass partition of 7.0 x 0.5 cm.

The chambers were made air tight with vaseline and desired humidities were maintained by means of sulfuric acid-water mixtures (Wilson 1921) placed on the floor of each chamber. A space of only about 2 mm below the false floor remained empty. Thus the relative humidity just above the gauze was close to the theoretical value for the sulfuric - acid - water mixture used.

Usually the humidity chambers were prepared on the evening prior to the experiments or were left undisturbed for at least 2 - 3 hours. Larvae were introduced and placed in the middle of each chamber either through the hole of the glass roof or by slightly lifting the upper half of the chamber. In similar experiments Hafez (1950) reported that the disturbed humidity equilibrium is soon re-established.

Type 2 chambers were used to determine the rate of crawling of individual larvae in several relative humidities. After half an hour, movements of an animal for fifteen minutes were recorded on squared paper. The upper lids of the chambers were marked off into squares to facilitate this recording. A stop watch was used to record one minute time marks on the tracks as well as the periods of inactivity lasting



more than one minute. The distances were measured with a map measurer and the average speed in cm/min was recorded.

For determining specific differences in activity of larvae type 1 and 2 chambers were used. Ten animals were used in each experiment and the activity, either for 15 minutes or at different intervals in the range of 0 - 60 minutes, were recorded.

Since certain soil insects under dry conditions are reported to lose water rapidly (Cameron 1917, Subklew 1934, Lees 1943), a few experiments were carried out to determine approximately the range of time over which larvae could survive in desiccated air. Small sulfuric acid desiccators (11 cm deep and 11 cm in diameter) at 21 - 22 C were used. Two batches of ten larvae each, were first washed in running water and then transferred to dry filter papers for 15 minutes prior to being weighed. During desiccation each batch was weighed at two hour intervals. The loss of weight was used to represent the water loss (Gunn 1933, Syrjämäki 1960).

Choice chambers of type 1 and 3 were used to determine the humidity preference of larvae. 5 - 20 animals were used in each experiment. The duration of each experiment was three hours. In order to eliminate any possible bias of the larvae due to light, the chambers were turned through 180° halfway through each experiment. Each experiment was repeated 5 - 10 times and a control (% R.H. 100 : 100) was used. The number of position records in each zone e.g. moister, drier and middle were noted. The excess percentage ratio  $100 (W - D) / (W + D)$  (Gunn and Cosway 1938) was employed to estimate the intensity of reaction. In this expression W and D are the numbers of the animals in the 'wet' and 'dry' sides respectively and the theoretical value for no reaction is 0.0%. For the purpose of comparison, the W/D ratio (Gunn 1937) was also calculated. In this, the value for no reaction is 1.0. The animals recorded from the middle zone were omitted from the calculations.

Experiments on the moisture of the substratum were carried out in the search for certain definite larval reactions and to relate the results with those obtained on uniform relative humidities. These were conducted in a 9 cm diameter petri dish. The bottom of the dish was covered with #1 Whatman filter paper which contained varying amounts of moisture. Percentage moisture was calculated as:  $100 \times (\text{wet weight} - \text{dry weight}) / \text{wet weight}$ . In each experiment one animal at a time was introduced into the petri dish for a period of 5 minutes. The following were calculated for each larva: (1) Average speed cm/min; (2) Average period of inactivity; (3) Number of wall climbings; (4) Number of burrowings; (5) Number of head capsule elevations; (6) Number of rollings.

#### Preliminary Experiments

In experiments with the constant humidity chambers both *C. furcata* and *C. mitis* show distinct reactions to low and high R.H. For example, in 50% R.H. and below the larvae remained strongly contracted for periods of 10 - 20 minutes. During contraction quick protrusion and retraction of the head capsule usually took place. The larvae seldom showed any crawling or burrowing movements although head movements were frequent. As a result dispersal from the center of the constant humidity



chambers was least in the range of 0 - 40% R.H.

In chambers of 80 - 100% R.H., the larvae usually showed active movement and remained burrowed under the glass beads whenever these were provided. The larvae also crawled up on the roof of the chamber and tended to rest there in high relative humidities.

When larvae were observed over periods of 30 minutes in the choice chamber apparatus (type 1), they showed a preference for one or the other side but did not remain in the moister side only. In most cases the larvae moved at random around the edge of the arena showing no behaviour suggestive of either a klinokinesis or klinotaxis.

A few experiments were carried out in constant humidity chambers of 0 - 100% R.H. to find the effect of desiccation. About 13 hours exposure at 24 C and approximately 0% R.H. was found to kill larval tabanids. It was also noticed that *C. mitis* was more active and sensitive to the effects of humidity than *C. fuscata*.

#### Variation in Activity and Rate of Movement with Humidity

##### *Variation between species*

The results obtained from data on 100 larval *C. mitis* are summarized in table 4. It can be seen that the activity increases as the relative humidity approaches 100%. This is in fair agreement with the observations made in preliminary experiments where the marked contraction of larvae at low humidities was noted.

TABLE 4. Activity of larval *Chrysops* in uniform humidities. The percentage of larvae active at various times. *C. mitis* at 25 C in type 1 chamber; *C. fuscata* at  $25.6 \pm 1.2$  C, in type 2 chamber; both at 85 foot-candles.

Time in minutes from placement of larvae in the chamber

	<i>C. mitis</i> (100)	<i>C. furcata</i> (6 x 10)								
	15	0	10	15	20	30	40	50	60	
% R. H.	Percentage of larvae active									
0	43	17	11	6	11	8	7	7	4	
10	42	20	21	19	18	16	7	7	11	
30	38	22	18	21	20	17	22	19	14	
60	70	29	27	27	27	28	28	31	30	
90	82	37	37	37	39	40	36	38	38	
100	-	25	35	42	38	45	34	35	41	

A more detailed series of experiments was carried out to examine the activity under various relative humidities. Ten larval *C. fuscata* were placed in the constant R.H. chambers and the number active and inactive were noted at 0, 10, 15, 20, 30, 40, 50, and 60 minutes. The data were obtained from 60 larvae which yielded 480 records. The results which are shown in table 4, demonstrate that the activity reaches a basal level after 30 minutes and that the larvae are more active in wet air than in

dry air.

The procedure for the two species which are summarized in table 4 differed in only one respect e.g., the types of the humidity chambers used. However, the percentage activity in the range of 0 - 90% R.H. for *C. mitis* is always found higher than for *C. furcata*.

*Variation in crawling rate with humidity*

The results are shown in table 5. The mean speed in cm/min increases with the increasing relative humidities and reaches a maximum at 100% R.H. Further, the mean period of inactivity decreases as the R.H. reaches saturation. The speed is almost constant in the range of 80 - 100% R.H. These results, however, present large individual variations. Another series of experiments was also conducted with five larvae which were selected on the basis of size and similarity of responses to various humidities. The results are given in table 5. Omitting the individual variations, the speed and the mean period of inactivity of larvae in the range of 10 - 100% R.H., seem to be good examples of an orthokinetic orientation (Fraenkel and Gunn 1940) in which the average speed of locomotion or the frequency of activity depends on the intensity of stimulation.

TABLE 5. The speed of movement of *Chrysops furcata* and periods of inactivity in uniform humidities in type 2 chambers at 85 foot-candles.

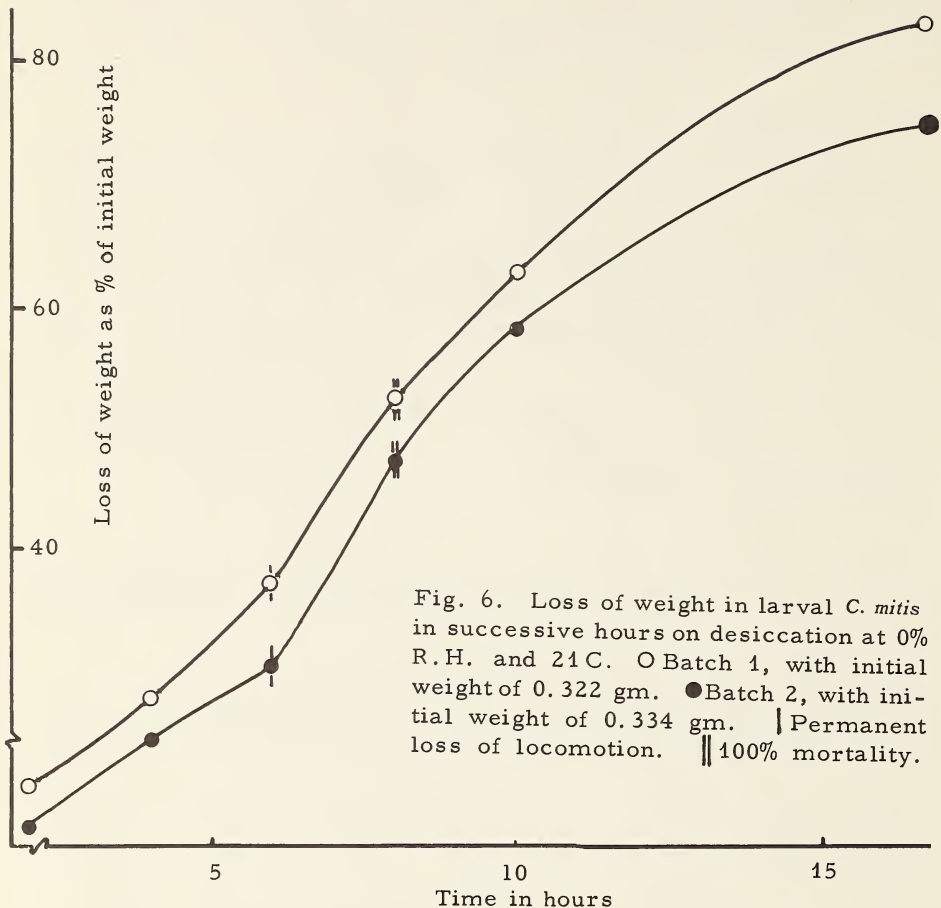
15 larvae at $27.1 \pm 1.6$ C				
% R. H.	Mean speed cm/min	SE	Mean period of inactivity	SE
10	0.55	0.14	6.7	1.6
40	0.61	0.18	7.2	1.4
80	1.20	0.30	4.1	1.3
90	1.24	0.20	2.9	1.0
100	1.64	0.31	1.7	0.6

5 larvae at $26.4 \pm 1.1$ C		
% R. H.	Mean speed cm/min	SE
10	0.16	0.15
40	0.21	0.19
80	1.03	0.47
90	0.86	0.29
100	1.05	0.34

**Rate of Moisture Loss**

Figure 6 shows the percentage loss of weight in *C. mitis* in successive hours during desiccation in dry air at 21°C. The weight of two batches showed almost no further change after desiccation for 18 hours. Accord-

ding to this the mean water content of larval *C. mitis* is 79.5%.



Desiccation begins to cause mortality of larvae very soon. After 6 hours of exposure to dry air (average weight loss 33.5%) most of the larvae were unable to move and 15% of them had already died. After 8 hours (average weight loss 49.5%) all the larvae were dead. The rate of water loss follows a sigmoid progress and the results confirm the preliminary observations that larvae cannot survive dry conditions for more than 13 hours.

#### Reactions in Humidity Choice Chambers

The results of 12 experiments are shown in table 6. The average mean excess percentage of all controls was 4.15% which roughly approximated the theoretical value for no reaction. The results show that below 50% R.H. larvae are quite unaffected by differences of 30% or even 40%

R.H., but they show some reaction when the alternative humidity offered is close to saturation. Thus some reaction is found in each of 100 : 90, 90 : 60, 90 : 40, 90 : 30, and 70 : 30 R.H. None of these reactions can, however, be regarded as intense except that of 90 : 30 where 61 larvae were recovered from the wet side, 29 from the dry side and the remaining 10 position records were from the middle zone. This partial avoidance of the dry side gives an excess percentage on the wet side of 35.5 and a W/D ratio of 2 : 1.

TABLE 6. Reactions of larval *Chrysops* to alternative relative humidities.

% R. H.		Position Records			Intensity of Reaction as:	
High	Low	Wet	Dry	Middle	Excess%	Ratio W/D
<i>C. furcata</i> , means of 5 experiments with 100 larvae at $25.6 \pm 0.6$ C, type 1 chamber, 85 foot-candles.						
100	90	53	38	9	16.5	1.4
100	80	44	47	9	-3.3	0.9
90	70	53	44	3	9.3	1.2
90	60	52	37	11	16.9	1.4
90	40	56	36	8	21.7	1.6
* 90	30	61, 54, 43	29, 36, 50	10, 10, 7	35.5, 20, -7.5	2.1, 1.5, 0.9
80	30	54	40	6	14.9	1.4
70	30	54	36	10	20.0	1.5
50	30	47	41	12	6.8	1.1
50	20	38	45	17	-8.4	0.8
50	10	44	51	5	-7.4	0.9
20	10	47	47	6	-1.1	1.0

*C. mitis*, means of 10 experiments with 50 larvae at  $26.1 \pm 0.6$  C, type 3 chamber, red light.

100	90	19	23	8	-9.5	0.8
100	80	27	21	2	12.5	1.3
90	70	18	28	4	-21.7	0.6
90	60	19	18	13	2.7	1.1
90	40	19	20	11	-2.6	0.9
90	30	22	21	7	2.3	1.0
80	30	22	25	3	-6.4	0.9
70	30	19	18	13	2.7	1.1
50	30	25	20	5	11.1	1.3
50	20	24	23	3	2.1	1.0
50	10	22	20	8	4.8	1.1
20	10	23	11	16	35.3	2.0

\* 90 : 30 experiment repeated and again repeated in the dark.



To check the above results it was thought necessary to use type 3 humidity choice chambers for another set of experiments. Since the animals are small and sluggish, the use of such chambers would decrease the space and consequently increase the frequency of larvae encountering the humidity boundary (Wellington 1960). Further, in these experiments, light as a variable factor was controlled by covering the humidity chambers with a piece of black cloth and the more active larval *C. mitis* were used. It was expected that under these conditions the humidity reaction of larvae might prove to be an intense one. The results of 12 such experiments are also summarized in table 6. The average mean excess percentage of all controls was 1.3 which approximated the theoretical value for no reaction. Thus neither the use of small alternative humidity chambers nor the control of light and the use of relatively active larvae improved the method for investigating the humidity reactions. However, still another set of experiments was conducted with the type 1 chamber in the hope of repeating the significant reaction in 90 : 30% R.H. The results of these experiments are also given in table 6. The data show that there is hardly any reaction over three hours in the dark. Clearly, larval *C. fuscata* and *C. mitis* show only a rather slight tendency to collect on the moister side.

#### Reactions to the Moisture Content of the Substratum

The results are included in table 7, and show that larvae move faster with increasing moisture. The tendency to burrow and to climb the wall of the container are also greater at higher percentage of moisture than at lower. On the other hand, period of inactivity, distinct elevation of the head capsule and inability to hold on the surface of the arena, e.g., rolling, are considerably higher at the lowest percentage moisture. Such behaviour appears to be due to physiological instability, perhaps caused by loss of water through evaporation. These results are consistent with those obtained in experiments with constant humidity chambers, where larvae seldom showed any rapid crawling or burrowing movement under low humidities.

#### Discussion

Most of the experiments were designed to find out whether there were any klinokinetic, klinotactic, or orthokinetic reactions of larval tabanids to moisture. No information on klinokinetic and klinotactic responses was obtained. However, as the percentage activity and speed in cm/min of the larvae increase with increasing moisture conditions and at the same time the mean period of inactivity decreases, a true orthokinesis is a major part of the orientation mechanism which would bring about aggregation of larval *C. mitis* and *C. fuscata* in a dry place if the results are to be interpreted in the conventional way. Such an explanation is confusing in view of the following facts: (1) In nature neither larval nor pupal stages of the species studied are found in dry places. (2) In the choice chamber apparatus larvae do not show any preference for the dry side; and (3) The inactivity and abnormal behaviour pattern of larvae in low R.H. and moisture percentage of substrate are obviously produced by the injurious effects of dry air. It follows that the hygro orthokinesis

could not possibly bring about larval aggregation in dry places. Now, moist soil is the preferred habitat of tabanid larvae and while the laboratory conditions included moisture, the soil with its associated factors (thigmotactic, textural, food, etc.) were absent. Therefore, the moist substrate in the laboratory experiments would tend to produce an orthokinetic reaction, since in moist soil the larvae are relatively inactive. Possibly then, the larvae are stimulated under moist conditions to react orthokinetically until the ideal conditions of moist soil are reached. Although the significance of such an orthokinetic reaction in terms of behaviour under natural conditions is open to question it seems likely that such a reaction would serve as a selective response during migratory phases of larvae from water to the bank of the pool and from the very moist soil to the slightly drier ground. Another possible explanation is that low moisture conditions would bring about temporary arrest of larval growth and consequently, no movement, while the activity of larvae could be brought on again by moist conditions. Such temporary arrest of activity during dry conditions and subsequently increased activity under moist conditions are quoted by Wigglesworth (1953) amongst larval stages of some Diptera.

TABLE 7. Types of activities of larval *C. mitis* under various percentages of moisture. Each figure represents 10 observations involving 50 larvae.

% Moisture	Mean speed cm/min	SE
2.3	$1.99 \pm 0.44$	0.13
12.0	$1.95 \pm 0.48$	0.15
24.4	$2.32 \pm 0.94$	0.29
41.5	$3.90 \pm 1.10$	0.34
77.5	$4.80 \pm 1.50$	0.47

The experiments on desiccation show that this is a real peril to larval tabanids. However, the initial contraction of the larval body wall in response to a continuous stimulus of low R.H. percentage seems to control water loss at least for a short time. The larva is incapable of maintaining the contracted condition after a certain amount of water is lost. These observations and the data on rapid loss of weight of *C. mitis* on desiccation indirectly support the view (Gunn 1933, Palmen and Suomalainen 1945) that most of the loss of weight of an arthropod on desiccation is due to evaporation of water from the integument.

#### TEMPERATURE REACTIONS OF LARVAL TABANIDS

The works of Miller (1929), Falconer (1945), and Hafez (1953) suggest that the rate of movement of larval insects is directly proportional to temperature over a wide range. Omardeen (1957) reported that

when second instar larvae of *Aedes aegypti* were subjected to a temperature gradient of 8 - 42 C, most larvae aggregated over the range of temperature 23 - 32 C. Third and fourth instar larvae and pupae showed a preference for 28 - 32 C. Literature pertinent to behavioural work with aquatic insects or forms living in semi-fluid media is scarce. I have studied activity and rate of crawling of larval *C. mitis* and *C. furcata* in relation to temperature. The temperature preference of *C. mitis* was also studied.

In the past, three kinds of observations have been made on the effects of temperature on the locomotory activity of insects. Shapley (1920) measured the speed of creeping of ants at various temperatures, the object being to find the 'normal range of temperatures for the locomotory activity'. Chapman *et al.* (1926), as quoted by Nicholson (1934), raised the temperature of a vessel containing various insects at a rate of 21 C per hour and recorded quantitatively the kinds of activity. Nicholson (1934) estimated the proportions of active or inactive individuals in several batches of blowflies under given temperature conditions. Shapley's and Nicholson's methods have been adopted for the present experiments. Omardeen's (1957) method slightly modified as described below was used for the temperature preference experiment.

#### Experimental Methods

Six constant temperature rooms at 5, 10, 15, 20, 25, and 30 C were used. Higher temperatures (35, 37, 40 and 42 C) were obtained by two water baths. Temperatures were checked before and after each experiment with a telethermometer. Glass plate temperatures obtained by the use of the water baths varied  $\pm 2$  C in time and  $\pm 0.8$  C over the plate and hence the average temperatures for these were recorded.

The animals used for the activity records consisted of two batches of ten larvae of *C. furcata*. These were stored at 10 C for twenty days in the dark. Before each experiment the larvae were transferred to a petri dish containing 1 cm of tapwater, and were then left at the constant temperature of the particular experiment for eight hours. For the higher temperature experiments the petri dish was placed on a glass plate suspended over a water bath. The first reading on crawling (criterion for activity) was taken after seven hours and four further readings were made at fifteen minute intervals. These readings were recorded during a period of 30 seconds each time on batches 1 and 2 with the help of a white diffuse light of 55 foot-candles and a red light of 2.5 foot-candles respectively.

Two batches of ten larvae each of *C. mitis* were used for determining the speed of movement at various temperatures. Observations were taken only after an animal had been at least two hours at the experimental temperature. However, one batch of larvae was exposed to the experimental temperature for 8 hours before readings were taken on speed of movement. Several glass plates up to 132 x 100 cm were used on which the larvae made their own trails. Again the glass plates were placed over a water bath for the high temperature experiments. Each larva was allowed to crawl for 15 minutes and the average speed in cm/min was recorded.



All experiments on the rate of movement were carried out in the dark. The only light used at the time of placing the larvae on the experimental glass plates was a red light of 2.5 foot-candles intensity. Since differences in speed between individuals were considerable in the dark, larval photonegative behaviour in a beam of horizontal light was utilized and a lateral light source of 55 foot-candles was used for one series of measurements to reduce the individual variations as well as to seek possible effects of light in combination with the experimental temperatures. Two batches of *C. furcata* larvae were used; one in the dark and one under a lateral light.

Temperature gradient experiments were carried out in an apparatus similar that as described by Omardeen (1957). This consisted of a thin sheet metal trough, 35.5 x 5 x 7 cm with 1 cm layer of 2 - 3 percent agar in tap water. The trough was fixed over a thick copper plate, 59.5 x 10 cm. An extended part, 7 x 5 cm, of the trough's floor was immersed in a freezing mixture of ice and salt, and cold water was circulated in the copper plate at the cold end. An electric flat immersion heater was used to heat the copper plate from the other end. Thus by cooling one end of the plate and heating the other a temperature gradient in the agar solution ranging from 9.7 - 34.8 C was maintained.

The floor of the trough was marked off into 14 sections of one inch each. The temperature at the middle of each section was measured with a telethermometer and the slope of the temperature gradient was found to be uniform and maintained almost constant over periods of two hours. A 47 x 10 cm fluorescent lamp was constantly used overhanging the trough. The light intensity on the floor of the trough was  $210 \pm 5$  foot-candles.

A hundred *C. mitis* larvae were used in the temperature preference experiments. These were stored at  $21.4 \pm .5$  C for two weeks prior to experimentation. Only those larvae which showed the least ill effects of heat were used. In each experiment ten larvae were evenly spread over section seven (20.8 C) of the trough and the numbers of larval positions in each section were counted at 5 minute intervals for 30 minutes. Each series of experiments was repeated ten times.

#### Activity and Speed at Uniform Temperatures

The results are summarized in fig. 7. It will be seen that at any temperature from 10 - 37 C the percentage activity in batch 1 recorded under a 55 foot-candles light was always higher than that in batch 2, the average increase being 32%. This obvious difference is attributed to the light. However, the two sets of data on the two batches are confirmatory to each other in so far as the activity under a normal range (15 - 25 C) of temperature is concerned. Neither batch shows any appreciable activity up to 10 C. At 15 C the activity suddenly rises in each batch and remains almost constant up to 25 C. The degree of constancy of activity in this temperature range (15 - 25 C) suggests that these temperatures are not harmful. This temperature range of 15 - 25 C appears to be the preferred zone of larval *C. furcata*.

At 37 C an average of 30 percent mortality was noted for each batch of larvae. The remaining 70 percent of the larvae at the end of the experiment at 42 C were also dead. Thus the temperature range of 37 -



42 C is lethal to the larval *C. furcata* under these conditions.

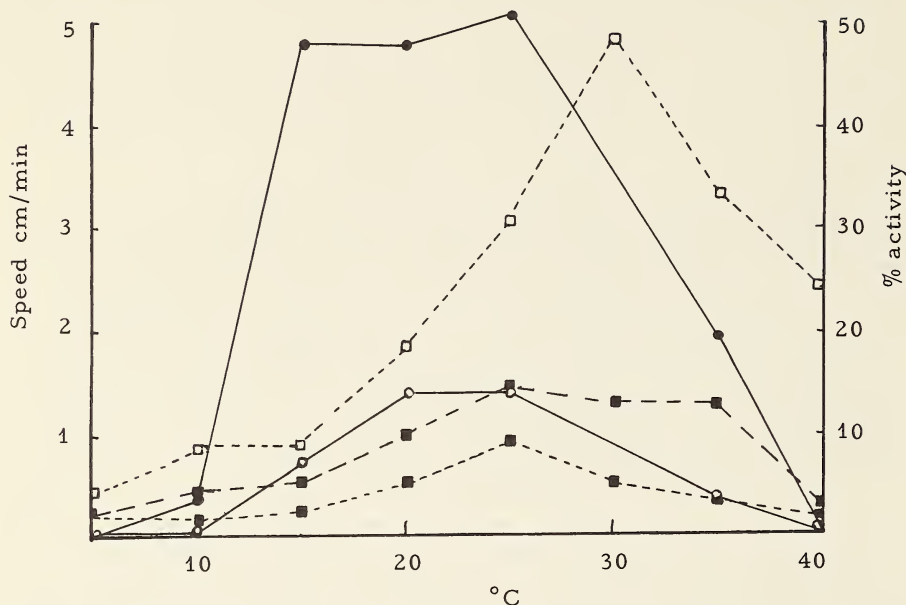


Fig. 7. Effect of temperature on the activity of larvae *C. furcata*, ○% activity under red light, ●% activity under white light, □ speed under lateral light, ■----speed in darkness; ■— larval *C. mitis* speed in darkness.

The mean values of speed cm/min of *C. mitis* increase very gradually in the temperature range of 5 - 25 C and are also included in fig. 7. The speed is roughly constant at 25 and 30 C and is decreased at 35 C and 40 C. Thus the temperature zone for maximum speed is 25 - 30 C.

The data obtained with the two batches with different pretreatment conditions prior to the experimental temperatures are closely similar. It seems, therefore, that such preconditioning has little influence on the rate of movement of the larval *C. mitis*.

The mean values of speed of *C. furcata* at any temperature for batch 2 are always higher than batch 1. Since the experimental conditions were the same for either batch except that the lateral light source was used for batch 2, it is obvious that the difference in speed is caused by the influence of light. Leaving aside the difference produced by light, the two series of data are closely similar to each other in respect to minimum speed at 5 C, increasing speed with increasing temperature and the amount of variation shown by the larvae. The temperature zones for maximum speed, however, are slightly different in each batch.

*C. mitis* shows a higher speed than *C. furcata* throughout the temperature range of 10 - 40 C. The rate of movement at 40 C does not diminish steeply. However, all larvae of both species died at 40 C.

### The Distribution of Larvae in the Temperature Gradient

The results of 40 experiments including the control and representing some 3000 position records are summarized in fig. 8. Under conditions of uniform temperature and illumination the larvae moved freely along the trough aggregating at both ends. This 'end effect' is clearly shown in the histogram for the control experiments.

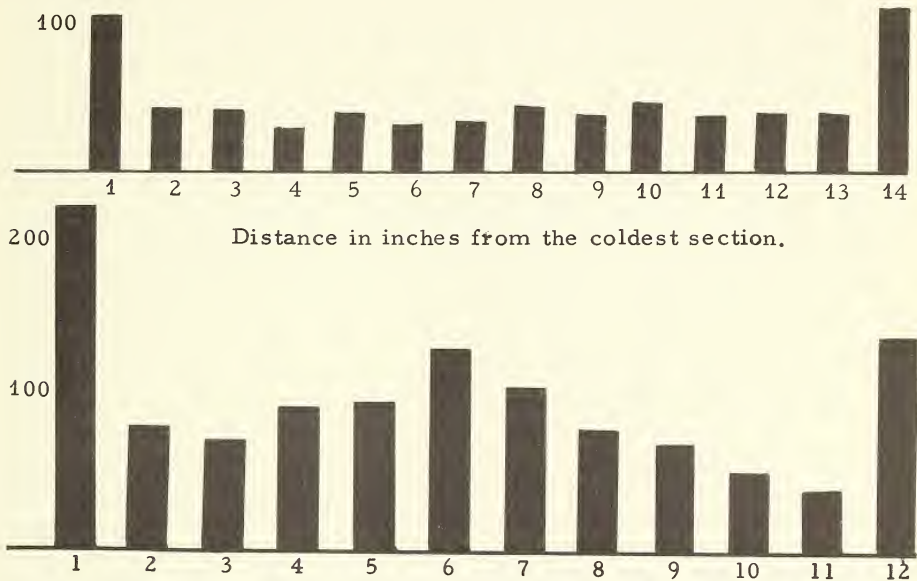


Fig. 8. The distribution of larval *C. mitis* in temperature-gradients; above, control, agar solution temperature constant at  $21.5 \pm 0.5^\circ\text{C}$ ; below, temperature-gradient  $17 - 31.5^\circ\text{C}$ , light intensity  $240 \pm 5$  foot-candles.

The temperature gradient experiments show that the larvae aggregate in the extreme cold end of the trough, the maximum number of position records being obtained from section 1 where the temperature was  $9.7^\circ\text{C}$ . The least number of position records appear between sections 6 - 13, until at the hottest end the distribution of larvae is fairly similar to those in sections 2 - 3. This distribution is due to different reactions displayed by the larvae at the two ends of the temperature gradient. Direct observations suggest that when larvae are first introduced into the gradient, they tend to move towards the hot end. But as time passes many of them turn by a 'trial and error' method of orientation and crawl towards the cold end. Some of the larvae do, however, reach the hottest end and are forced to remain there by the pathological effects of heat. All larvae on reaching the hottest end showed increased rate of movement and an occasional tendency to climb and burrow for awhile. With time, however, the behaviour changed to rapid probing, coiling, and rolling suggesting stages of distress and loss of control. Few larvae under these conditions, could move in the direction of the

cold end of the gradient. On the other hand, the aggregation at the coldest end occurs owing to slow movement and decreasing activity of larvae with time. Further observations suggest that larval aggregation is also influenced to a great extent by the 'end effect' at the coldest end. This end effect was different from that of the hottest end since larvae here formed inactive groups mainly in the corners of the trough; thigmotaxis appears to be a potent factor in producing larval aggregations at the coldest region. The importance of cold, however, is supported by the results as shown in fig. 7 where the least percentage activity and speed in cm/min have already been demonstrated in the uniform temperature range of 5 - 10 C.

Larval *C. mitis* do not exhibit any clear 'temperature preference' under these experimental conditions, perhaps because of the steepness of the temperature gradient. A few experiments were carried out with the same batch of larvae but in a temperature gradient where the temperature ranged from 17 - 31.5 C representing only twelve one inch sections of the metal trough. Ten larvae were evenly spread over section six of the trough and the number of the larval positions counted in each section at 5 minute intervals for 60 minutes. The increase in recording time increased the chances of a larva coming into contact with all the parts of the temperature gradient several times. The histogram for this series of experiments is of comparable significance with the others since each is based on 1200 position records. A comparison shows: (1) a slight increase in the number of position records at the hottest end; but (2) a considerable decrease in the number of position records at the coldest end; and (3) the presence of a middle range of larval aggregation at a temperature of 22 - 24 C. These differences in the distribution pattern are attributable to the difference in temperature range and slope of the gradient. Larval *C. mitis* in the 17 - 31.5 C gradient showed continuous activity both at the cold and the hot end of the gradient. Observations, however, again indicated that aggregations at the ends are mainly attributable to thigmotaxis. Among the larvae remaining outside the cold and hot sections the temperature zone of 22 - 24 C appears to be preferred.

### Discussion

Various workers (Shapley 1924, Crozier and Stier 1925, Bodenheimer and Klien 1930, Falconer 1945, and Hafez 1950) have analyzed their data on the rate of movement of insects on the basis of the  $Q_{10}$  rule or the Arrhenius equation (Crozier 1924). The values of  $Q_{10}$  and the critical increment ( $\mu$ ) for the Arrhenius equation are about 2 - 3 and 10,000 - 18,000 respectively. Examination of the curves in fig. 7 shows no resemblance to the usual type of  $Q_{10}$  or Arrhenius curve except between 10 - 30 C. This partial resemblance of the curves to the  $Q_{10}$  curve is to be expected since Miller's (1929) study on *Lucilia* larvae and Crozier and Stier's (1925) work on the caterpillars of *Malacosoma* sp., suggest that the frequency of muscular contraction varies directly with the experimental temperatures but the amplitude of contraction waves is constant in the normal range of temperature and decreases outside these limits. Since the normal range of temperature for larval tabanid activity

appears to be 10 - 30 C the decrease in the rate of movement outside this temperature zone seems quite logical. These results support the views of Uvarov (1934) and Mellanby (1939) that the rate of movement or activities of insects within the normal limits is not constant but increases with rising temperature.

The larval aggregation in sections 6 - 7 of the gradient, which had a mean temperature of 23 C has been suggested as due to a true temperature preference of the larvae. Since the other reactions to temperature described suggest a number of normal ranges of temperature for larval tabanids a 'temperature preference value' was calculated from the data obtained with the temperature gradients, using the procedure recommended by Herter (1953). The numbers of larvae recorded from the ends of the gradients were omitted since such larval positions were due to end effects. The maximum activity temperatures range from 21.9 - 28.4 C and, under laboratory conditions, lateral light produces a most noticeable effect. The 'temperature preference' values vary little and range from 19.3 - 24.4 C with a mean of  $21.4 \pm 0.8$  C. This is in close agreement with the value 23 C obtained from the temperature gradient experiments directly.

#### GENERAL CONCLUSIONS

Although larval tabanids were exposed to simplified conditions of light, temperature, humidity, and moisture which are not separable in nature, the results obtained in the foregoing sections can be related to the ecology of the larvae in their normal environment.

Very few soil burrowing insects are other than negatively phototactic (Cameron 1947). Larval tabanids react to light either by crawling or by suddenly withdrawing the head capsule. A general sensitivity to light resulting in motor response would keep the larvae buried in the soil and consequently protect them against wandering into illuminated areas where they would be exposed to predators and desiccation. This may be why even the pupae are found covered under leaves or vegetation.

Reaction time experiments showed that larvae are able to integrate light energy over periods of seconds and to utilize the effect to produce a directional response. Several eyeless animals have been shown to possess this ability (North 1957). The mechanism of integration of light might be of advantage to a larva in the dark environment especially when it is migrating to the soil surface for pupation.

No directed reaction to dry or wet air was observed in several different types of humidity gradients. These negative results are not at all surprising since it is well known that the larvae live in a microclimate which is typically moist and perhaps they do not possess the ability of hygrotactic orientation. Their presence in moist habitats can be explained as a result of direct selection of such places by the ovipositing female tabanids.

A consistent inactivity under low percentage of R.H. and moisture is shown by larval tabanids. Such a reaction under natural conditions seems especially important for aestivating larvae in which inactivity



would be induced by the dryness of the environment and greater activity by increasing moisture of the soil. Variable activity of this nature dependent on moisture percentage has been reported in many soil insects (Uvarov 1934).

Published data show that the mean maximum temperature for July from the surface to any depth of the soil down to 50 cm does not exceed 23 C in any of my collecting sites. Since the experimentally determined lethal temperature for larval tabanids is 37 - 42 C, high temperature cannot limit the distribution of these larval tabanids in the soil in Alberta.

Hibernating larval tabanids are subject to temperatures down to -3 C in southern Alberta and -8 C in northern Alberta, if we assume that larvae migrate down to 20 cm below the soil surface (Cameron 1917). Although no experiment was conducted below 5 C, at 5 - 10 C larval activity varied from 0 - 4% while the rate of crawling was 0.2 cm/min and larvae in the soil at and below 5 C become sluggish and quiescent and do not pupate. It seems likely that a temperature of 5 C or lower initiates hibernation. The temperature preference of the mature larvae was found to be  $21.4 \pm 0.8$  C, a temperature which is common during June - August, the period of maximum activity of larval tabanids under field conditions.

On the basis of the laboratory findings it seems impossible to assess the relative contribution made by each of the foregoing physical factors to general behaviour of the larva in its normal habitat. But it is highly probable that in swamps, pools and lakes, where there is no risk of desiccation, light and temperature are the most important environmental factors influencing the behaviour of the larvae.

Variation in response of larval tabanids to physical factors was a common feature in this study. It was not possible to use laboratory reared larvae since no suitable means of rearing larvae from the eggs are known. Although it was possible to collect larvae in adequate numbers, standardization of larvae for testing in the laboratory was a problem. The response of larvae to light varied somewhat with age; for example, immature ones may be indifferent to lateral light, mature ones show intense negative phototaxis, whereas those which are about to pupate are more light tolerant. It was, therefore, possible to select larvae of almost uniform sensitivity for light experiments. Screening methods were not applicable in humidity, moisture, and temperature experiments since no directed reaction was obtained for these conditions.

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## EFFECTS OF FUMIGANTS ON THE RESPIRATORY MECHANISMS OF *TENEBRIO MOLITOR* (L.)

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Fumigation of larvae and adults of *Tenebrio molitor* (L.) for five hours with ethylene dichloride at 0.12 gm/l resulted in an apparent increase in oxygen consumption during treatment. Sorption of the fumigant by the insect tissue caused a decrease in pressure in the manometer which would ordinarily be construed as an increase in oxygen consumption. A 45 minute treatment caused hyperactivity and an increase in ventilation movements in larvae resulting in an increase in oxygen consumption. Paralyzed adults and anaesthetized insects showed no change in oxygen consumption after treatment but high doses of ethylene dichloride depressed oxygen consumption by homogenized tissue. Similar treatment with carbon disulphide caused no significant change of oxygen consumption in adults or larvae, but larvae were paralyzed sooner than by ethylene dichloride. Carbon disulphide depressed oxygen consumption by anaesthetized insects and by homogenized tissue, the effect being greater at higher doses. Sorption of carbon disulphide was faster than that of ethylene dichloride. Both fumigants caused the second and third spiracles of *Tenebrio molitor* adults to open when applied locally to the ventral nerve cord.

Fumigants are toxic chemicals which enter the bodies of insects in gas form, chiefly through the spiracles, but also through the integument (Bond 1961). The opening and closing of the spiracles is the chief factor controlling the amount of fumigant which enters the body. Since the respiratory rate is closely correlated with these spiracular movements, fumigants affect it. For example, the susceptibility of insects to methyl bromide is closely related with the respiratory rate (Bond 1956) and hydrogen cyanide, which is a respiratory poison acting on the cytochrome system, increases the resistance of some insects to methyl bromide (Bond 1961).

The finding that carbon dioxide can affect the movement of isolated or denervated spiracles (Beckel & Schneiderman 1957, Case 1957, Miller 1960b, Hoyle 1961) through neuromuscular transmission (Hoyle 1960) raises the question as to whether fumigants affect spiracular movement irrespective of their effects on the rate of respiration. Bond (1961) found it difficult to attribute spiracular condition to any particular action of the fumigant or to relate uptake of the fumigant to the spiracular condition. Kitchel & Hoskin (1935) found an irregular response of the spiracles of Hawaiian cockroaches *Nyctobora noctivaga* (Rehn) to nicotine concluding that nicotine deranges the mechanism of spiracle control. Wigglesworth (1941) showed that the spiracles of *Cimex lectularius* were closed most of the time when paralysis caused by pyrethrins was complete.

Shafer (1911, 1915) found that, when a tissue extract of *Passalus cornutus* Fab. was treated with carbon disulphide, oxygen consumption was depressed and oxidase and catalase strongly inhibited. DeMeio & Brieger (1949) found that rabbit kidney, liver, and brain tissues treated with 0.01 M carbon disulphide, showed no decrease in oxygen consumption, but carbon disulphide reacts with reduced glutathione (Anonymous

1949), affects oxidase and catalase (Shafer 1915), and inhibits the succinic oxidase enzyme system (McKee *et al.* 1943).

The effect of ethylene dichloride on insect respiration has not been studied. Working on *Musca domestica* L., Winteringham & Hellyer (1954) found that ethylene dichloride vapour induced deep narcosis within 5 minutes, with only a very slight fall in the levels of adenosine triphosphate and arginine phosphate. Exposure for one hour caused considerable depletion of ATP and arginine phosphate but the phosphoglycerate level was unaffected. They concluded that the delayed depletion of adenosine triphosphate by ethylene dichloride indicates that narcotics impede the oxidative synthesis of this material but the immediate narcosis with little depletion of ATP within the first few minutes does not support this view. Furthermore, ethylene dichloride does not react with reduced glutathione (Anonymous 1949). This indirect evidence indicates that ethylene dichloride is not likely to affect the respiration of insects.

## MATERIALS AND METHODS

I measured oxygen consumption by *Tenebrio molitor* L. during treatment with fumigants; some of the insects were first treated with fumigants, then their oxygen consumption was determined. The insects were classified as active if they still moved, or paralysed if they were lying on their sides or backs, to assess the part played by activity in the variations in oxygen consumption observed. The larvae were better for this study because they are not so readily paralysed. To eliminate the effect of activity oxygen consumptions by homogenized tissue and by anaesthetized insects were determined after treatment with fumigants. The effect of fumigants on ventilation prior to paralysis was observed. After paralysis, the condition of spiracles is the chief factor affecting the amount of fumigants entering the body and so this was also recorded.

The insects were obtained from a culture reared at 26 C. About twenty-four hours before the test, the insects were put in separate containers without food. Mature larvae of *Tenebrio molitor* L. and adults three to six days after emergence were used.

### Oxygen Consumption

Oxygen consumption was measured in a Warburg constant volume respirometer with one insect in each flask. Carbon dioxide was removed by filter paper soaked with 0.1 ml of 10% potassium hydroxide in the center well. The experiments were run at 25 C. Oxygen consumption before fumigation was determined first and then the air in the manometer and flask was replaced by a fumigant-air mixture. The method used was essentially that of Umbreit *et al.* (1964). The manometers were connected together with plastic tubes. The last manometer was connected to a flask containing fumigant-air mixture and the first manometer to a vacuum line with a side arm to a manometer for measuring absolute pressure in the whole system. The rubber tubes which served as reservoirs for Brodie's fluid at the lower ends of the manometers were clipped at the upper ends to prevent the rising of the fluid into the manometers when



the system was under vacuum. The whole system was first evacuated to an absolute pressure of 6 cm mercury or lower and then refilled with fumigant-air mixture. This was repeated three times and then the mixture was continuously flushed through the system for ten minutes. The system was closed and ten minutes allowed for temperature equilibration before oxygen consumption was measured for the balance of the 5 hr fumigation period. For measuring the oxygen consumption after fumigation, the air was replaced by the fumigant-air mixture, the system was closed for 45 minutes, and the mixture was then replaced by air. In each of these tests, two of the tubes served to measure the respiration of control insects. Oxygen consumption over successive 30 minute periods was determined in all tests. Between tests respiratory manometers were disconnected, each flask was aerated, and filter papers moistened with potassium hydroxide were replaced.

To obtain a desired concentration of fumigant, the calculated quantity was injected with a micro-syringe into a 6.7 litre flask evacuated to half atmospheric pressure or lower. The flask was fitted with a rubber bung with 2 holes. One of these carried two glass stopcocks leading to the respirometer and joined by a rubber coupling; the fumigant was injected through the hole in the second stopcock, which was disconnected for this purpose. The second carried a glass tube to the bottom of the flask, coupled to the water supply and controlled by a clamp. The rubber stopper of the flask was covered with aluminum foil to prevent sorption of fumigant by the rubber. Water was run into the flask when fumigant was flushed through the respirometer.

Tissue homogenates were prepared by grinding the tissue with a homogenizer in Krebs-Ringer's phosphate solution buffered at pH 6.7 (Umbreit *et al.* 1964) which is about the middle of the pH range of tissues of *T. molitor* (Roeder 1953). For each test, ten adults or six larvae were used and the homogenate was prepared in 25 ml of buffer solution. The homogenate was filtered through several layers of cheese cloth to eliminate fragments of cuticle. About two-thirds of the tissue homogenate was then transferred to a vial which was put into a copper-screen tube with a diameter of 2.8 cm and height 7.5 cm. Then the homogenate was exposed to a known concentration of fumigant for a period of time, after the method of Richardson & Casanges (1942). The fumigant was injected into a 3.1 litre Erlenmeyer flask as described above. After vapourization was complete and air had been flushed in, the original stopper was replaced quickly with another stopper, from which the copper-screen tube with the vial containing homogenate was suspended. After treatment, the homogenate was placed in the respiratory flasks which were weighed previously and the flasks with the homogenate were weighed again. The oxygen consumption by the homogenate of four treated and three control samples was then determined. The pH of the homogenate was measured before and after treatment with fumigant and also after oxygen consumption was measured and it remained stable in the treated and control samples.

For studying the effects of fumigants on oxygen consumption by insects anaesthetized with chloroform, some adults and larvae were first anaesthetized by putting them into a flask saturated with chloroform and



removing them after they became motionless. They were then treated with ethylene dichloride or carbon disulphide for 0.75 hour and their oxygen consumption over a period of one hour was measured. The control insects were similarly anaesthetized with chloroform before their oxygen consumption was determined. Homogenized larval tissue was treated with chloroform saturated in air for 0.25 hour to see if chloroform affects tissue respiration. Four treated and three control samples were used.

#### **Sorption by Insects**

To see whether the insects themselves remove any quantity of fumigants during treatment, the insects were put into a copper-screen tube with cover, exposed to a known concentration of fumigant and weighed at intervals. To minimize water loss from the insects, the relative humidity in the flask was kept high by 5 ml of water run into the flask on the day before the test.

#### **Respiratory Movements**

A petri dish with the upper rim greased before covering was used to contain insects while spiracular movements were observed under a binocular microscope. The test insect with wings removed to expose the spiracles was mounted on a piece of molding clay and the fumigant was injected with a micro-syringe onto a small piece of cotton wool in the petri dish to give concentrations of 0.12 and 0.24 gm/l, and allowed to vapourize. Spiracles with associated structures were also dissected from the insects and placed on a small cotton ball soaked with Ringer's solution in a petri dish to which fumigant was introduced. Observations on the effects of fumigants on abdominal ventilation movements were made in the same way.

Observations on the time to paralysis were made by exposing insects to a known concentration of fumigant in an Erlenmeyer flask as with homogenized tissue.

To study the effect of ethylene dichloride and carbon disulphide on the activity of the ventral nerve cord, male *Periplaneta americana* (L.) adults were used. They were decapitated, mounted in a wax dissecting dish, and the body was opened through the dorsum exposing the ventral nerve cord which was then slightly raised and placed on a pair of platinum wire electrodes leading to an oscilloscope.

## **RESULTS**

#### **Oxygen Consumption during Fumigation**

Both sexes of *T. molitor* adults showed an initial increase of oxygen consumption one hour after the treatment with ethylene dichloride started at a concentration of 0.12 gm/l (0.0012 M), the increase being more pronounced in the males than in the females (fig. 1). Oxygen consumption reached its peak one hour after the treatment started, and gradually decreased reaching its original level an hour after treatment finished. When the treatment was just started, the beetles showed more activity.

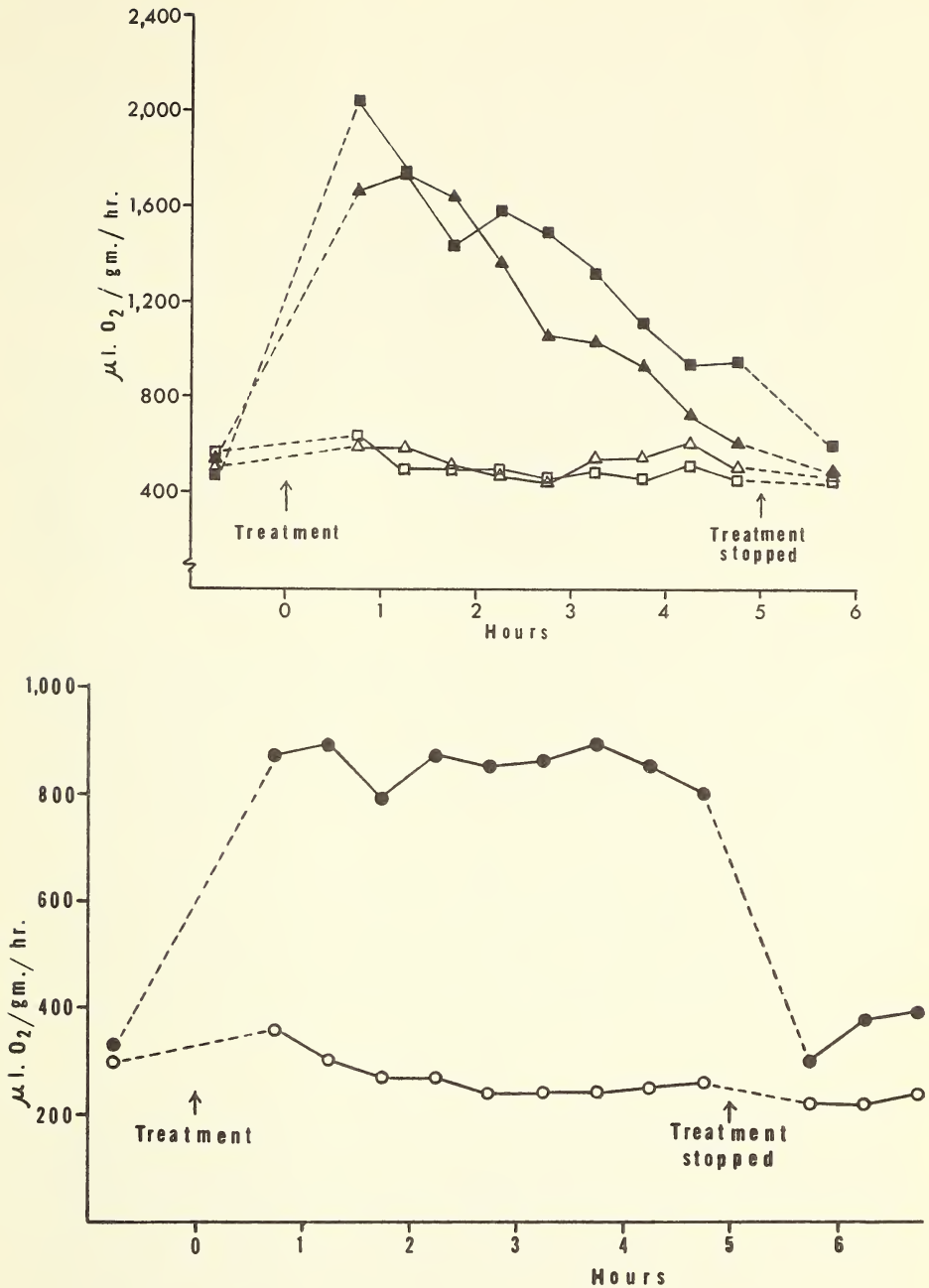


Fig. 1. Mean oxygen consumption by *Tenebrio molitor* before, during and after fumigation with ethylene dichloride (0.12 gm/l.). Upper: adults; lower: larvae. ■ 7 treated males, □ 2 control males; ▲ 7 treated females, Δ 2 control females; ● 7 treated; ○ 2 control insects.

This probably would not account for all of the increase in oxygen consumption because most were paralysed in less than fifteen minutes.

When the larvae were fumigated with the same concentration of ethylene dichloride, there was an increase in oxygen consumption and this was maintained throughout the whole fumigation period (fig. 1). There was a sharp drop towards the original level after the treatment stopped. After fumigation started, hyperactivity occurred for some time before paralysis set in. These restless movements lasted for an hour or longer accounting for part of the increase in oxygen consumption. Part of the pressure change may have been due to sorption of the fumigant by the insects, since there was a sharp drop in apparent oxygen consumption when fumigation stopped.

Fig. 2 shows the results when the adults were fumigated with carbon disulphide at a concentration of 0.12 gm/l (0.0016 M). The males and females showed no marked changes of oxygen consumption in comparison with the controls during and after the treatment. Fig. 2 also shows the oxygen consumption rate during the period when the larvae were fumigated with carbon disulphide at a concentration of 0.12 gm/l. A sudden increase was followed by a sharp decrease and two hours after fumigation started, the rate of oxygen consumption by the treated insects was essentially the same as that by the control.

#### Oxygen Consumption after Treatment

As shown in fig. 3, there were wide variations among the individuals in oxygen consumption after treatment with ethylene dichloride which did not correlate with the insects' activities. However, when an insect was incapacitated immediately after treatment, there were some spasms, although no increase of oxygen consumption. When hyperactivity occurred for a longer period there was a corresponding higher rate of oxygen consumption.

When the adult females were similarly treated, there was essentially no difference in oxygen consumption between the treated and the control (fig. 4). The insects were all paralysed after the treatment.

Another lot of larvae was similarly treated with carbon disulphide (fig. 4). There was no hyperactivity or increase of oxygen consumption after the treatment. Similar results were obtained with adult females (fig. 4).

#### Effects on Homogenized Tissue

Ethylene dichloride at 0.12 gm/l x 1 hr greatly increased the oxygen consumption by most of the *Tenebrio molitor* larvae through its irritating effect, but this dosage depressed slightly the consumption by larval tissue homogenates. A higher dosage was required to depress the oxygen consumption by homogenized tissue of adult males and females (table 1). Carbon disulphide at 0.12 gm/l x 1 hr depressed the oxygen consumption by homogenized tissue of larvae and of adults of both sexes, the effect being greater in adults.

#### Effects on Anaesthetized Insects

Carbon disulphide depressed the oxygen consumption by both the

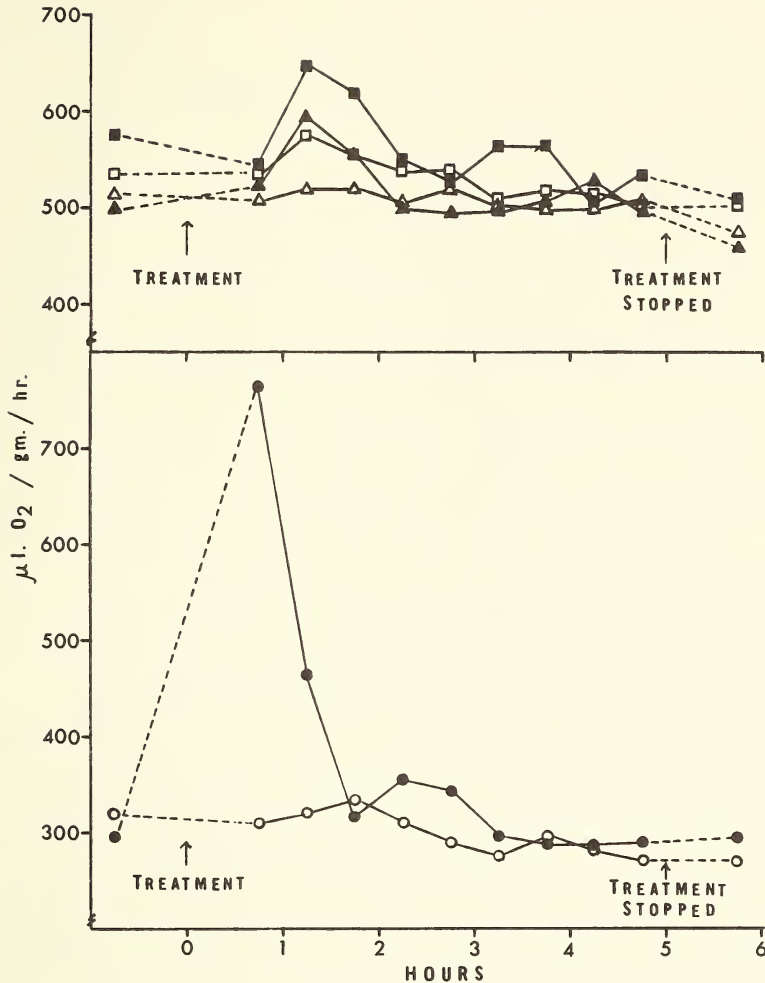


Fig. 2. Mean oxygen consumption by *Tenebrio molitor* before, during and after fumigation with carbon disulphide (0.12 gm/l.) for 5 hours. Upper: adults; lower: larvae. ■ 7 treated males, □ 2 control males; ▲ 7 treated females, △ 2 control females; ● 7 treated larvae, ○ 2 control larvae.

adults and larvae anaesthetized with chloroform whereas ethylene dichloride produced no significant effect (table 2). The legs of the adults treated with ethylene dichloride and carbon disulphide and those of control adults were folded, indicating tetanic contraction of the muscles.



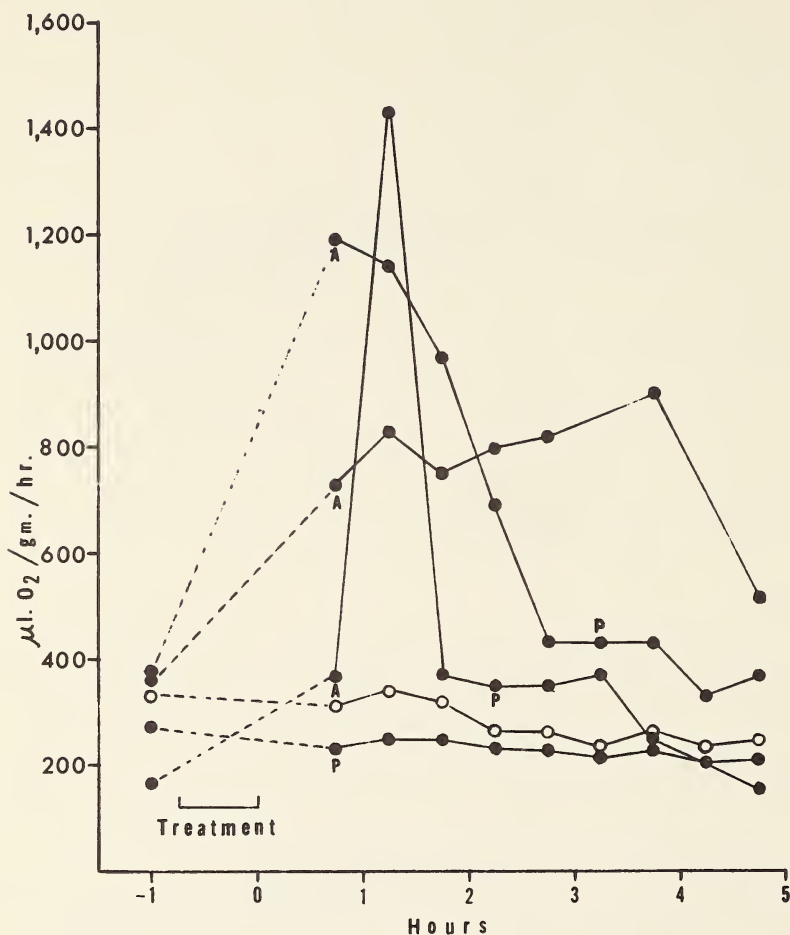


Fig. 3. Oxygen consumption by *Tenebrio molitor* larvae before and after treatment with ethylene dichloride (0.12 gm/l.) for 0.75 hour. ● treated; ○ control insect. A = active; P = paralysed.

Chloroform was found not to affect oxygen consumption of homogenized tissue of larvae after these were treated for 0.25 hr. The oxygen consumption by the control samples was  $41 \pm 6.1 \mu\text{l O}_2 \text{ gm/hr}$  and that of treated samples was  $38 \pm 4.2 \mu\text{l O}_2 \text{ gm/hr}$  as determined over a period of 2.5 hours.

#### Sorption of Fumigants by Insects

No further sorption of carbon disulphide by adult females occurred after 40 minutes or by larvae after 80 minutes (table 3). In each stage

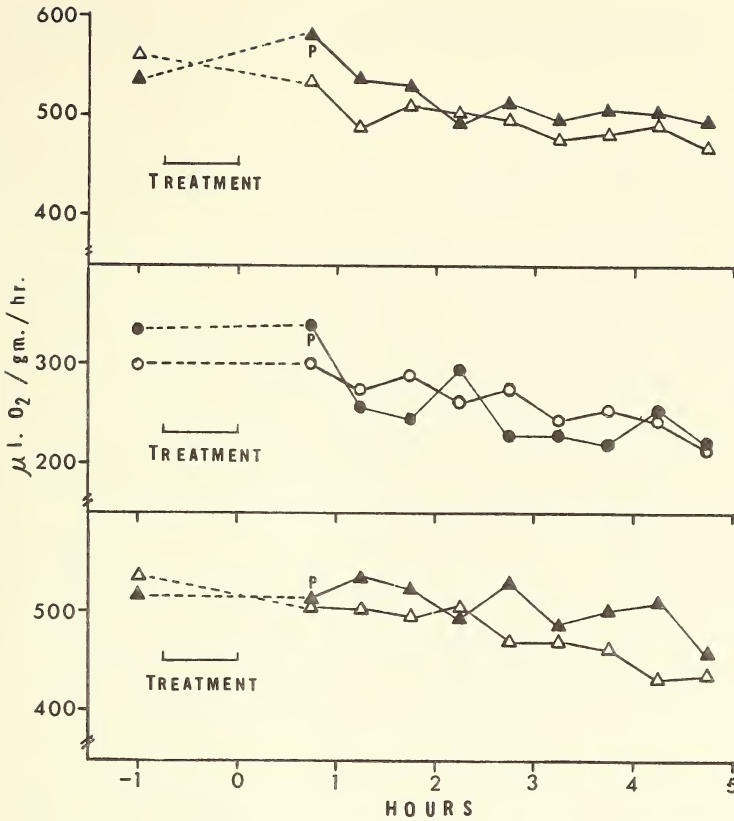


Fig. 4. Mean oxygen consumption by *Tenebrio molitor* before and after treatment. Upper: females, treated with ethylene dichloride (0.12 gm/l.) for 0.75 hr. Middle: larvae; Lower: females, both treated with carbon disulphide (0.12 gm/l.) for 0.75 hr.  $\blacktriangle$  7 treated females,  $\triangle$  2 control females;  $\bullet$  7 treated larvae,  $\circ$  2 control larvae. P = paralysed.

most of the sorption took place within the first half of this period. Sorption of ethylene dichloride was much slower; there was no detectable change of weight of larvae in the first 20 minutes. Sorption of both materials was much quicker in adults than in larvae.

#### Effects on Abdominal Ventilation

In *T. molitor* adults, the normal ventilation mechanism is raising and lowering of the abdominal terga supplemented by protraction and retraction of the head and prothorax and longitudinal telescoping movement of the last few abdominal segments. When they were fixed to the molding clay, they struggled to free themselves and demonstrated the three types of ventilating mechanisms. For each test, two males and two females were used and the movements of the abdominal terga only were counted.

TABLE 1. Effects of fumigants on the oxygen consumption by homogenized tissue of adults and larvae of *Tenebrio molitor* 3 control and 4 treated samples in each test.

Test No.	Stage & sex	Fumi-gant	Dosages gm/lxhr	O <sub>2</sub> Consump. $\mu\text{l O}_2/\text{gm/hr}$	Period hrs.	t test value	Prob. of t
1	larv.	control		496.3 $\pm$ 15.9	6.5		
	larv.	EDC	0.12 x 1	429.4 $\pm$ 17.4	6.5	3.45	> 0.01
	larv.	CS <sub>2</sub>	0.12 x 1	402.7 $\pm$ 9.9	6.5	5.29	< 0.01
2	larv.	control		472.7 $\pm$ 3.9	6.0		
	larv.	CS <sub>2</sub>	0.18 x 2	351.6 $\pm$ 22.9	6.0	5.17	< 0.01
3	larv.	control		240.6 $\pm$ 8.0	5.5		
	larv.	EDC	0.18 x 2	132.1 $\pm$ 3.2	5.5	7.02	< 0.001
4	♀	control		461.2 $\pm$ 23.1	7.0		
	♀	EDC	0.12 x 1	449.3 $\pm$ 13.2	7.0	0.40	> 0.5
	♀	CS <sub>2</sub>	0.12 x 1	341.3 $\pm$ 12.3	7.0	4.95	< 0.01
5	♂	control		385.4 $\pm$ 7.3	5.5		
	♂	EDC	0.18 x 2	305.1 $\pm$ 9.3	5.5	6.09	< 0.01
	♂	CS <sub>2</sub>	0.18 x 2	214.5 $\pm$ 8.0	5.5	14.12	< 0.001
6	♀	control		562.6 $\pm$ 16.3	5.5		
	♀	CS <sub>2</sub>	0.18 x 2	323.1 $\pm$ 7.5	5.5	17.40	< 0.001

EDC = ethylene dichloride

TABLE 2. Effects of fumigants on oxygen consumption by *Tenebrio molitor* anaesthetized with chloroform as determined over a period of 1 hour. 10 control and 10 treated insects in each test.

Test No.	Stage & sex	Fumi-gant	Dosages gm/lxhr	O <sub>2</sub> Consump. $\mu\text{l O}_2/\text{gm}$	t test value	Prob. of t
1	larvae	control		316.1 $\pm$ 10.9		
	larvae	EDC	0.12 x 1	293.1 $\pm$ 12.8	1.37	> 0.1
	larvae	CS <sub>2</sub>	0.12 x 1	238.3 $\pm$ 12.9	4.59	< 0.001
2	females	control		639.5 $\pm$ 19.2		
	females	EDC	0.12 x 1	601.9 $\pm$ 22.3	1.28	> 0.2
	females	CS <sub>2</sub>	0.12 x 1	470.7 $\pm$ 13.5	7.21	< 0.001

EDC = ethylene dichloride

TABLE 3. Cumulative increase in weight of *Tenebrio molitor* due to sorption of fumigants during treatment.

Stage		Time (min.)	Total wt. gained mg.
CS <sub>2</sub>	females (10)*	20	12.7
		40	14.2
	larvae (8)	20	8.0
		40	15.3
		80	20.8
EDC	females (10)	20	2.3
		40	5.3
		70	11.5
		130	18.4
		190	24.4
		250	28.2
	larvae (8)	20	nil
		40	1.6
		70	7.5
		130	15.1
		190	25.2
		250	36.0
		310	46.1

EDC = ethylene dichloride

\* Figures in parentheses indicate the number of specimens.

Before ethylene dichloride was introduced into the chamber, the number of ventilation movements per minute was  $18 \pm 1$  and after treatment, it increased to  $26 \pm 2$  before they were paralysed when all movements stopped. When carbon disulphide was used, the abdominal tergal movements per minute before and after treatment were  $19 \pm 2$  and  $20 \pm 2$  respectively.

#### Time to Paralysis

Ten specimens of both larvae and adults were used to determine the length of time for paralysis to set in after treatment with ethylene dichloride and carbon disulphide. When the adults were on their backs with no movement of legs, and when the larvae showed only occasional very slow bending movements of the bodies, they were assumed to be paralysed. Table 4 shows that carbon disulphide paralysed larvae quicker than ethylene dichloride. Although both paralysed the adults faster than the larvae, the effect was more pronounced in ethylene dichloride. The time required for carbon disulphide to paralyse the larvae was less than twice that for paralysing the adults but the time required for ethylene



TABLE 4. Time in minutes to paralysis of *Tenebrio molitor* during exposure to fumigants.

Stage & sex	Fumigants	Time, mean (of 10) $\pm$ S. E.
0.12 gm/l		
larvae	carbon disulphide	18.0 $\pm$ 0.6
females	carbon disulphide	12.3 $\pm$ 0.3
males	carbon disulphide	13.1 $\pm$ 0.6
larvae	ethylene dichloride	65*
females	ethylene dichloride	12.0 $\pm$ 0.4
males	ethylene dichloride	13.3 $\pm$ 0.5
0.24 gm/l		
larvae	carbon disulphide	7.0 $\pm$ 0.5
females	carbon disulphide	4.6 $\pm$ 0.2
larvae	ethylene dichloride	35*
females	ethylene dichloride	4.5 $\pm$ 0.2

\* To paralysis of all 10 specimens.

dichloride to paralyse the larvae was five times as long as for paralysing the adults.

#### Responses of the Spiracles of Adults to Fumigants

Observations were made only on the second and third pairs of spiracles because they are easy to see with the microscope. The second spiracle, located just posterior to the base of the elytron, is a trough-like structure dilated by a single muscle attached obliquely to a sclerotized bar along the anterior edge of the spiracular opening. The third spiracle, located on the first abdominal segment and posterior to the hind wing base, has a single valve-type closing apparatus (Snodgrass 1935). The anterior bar forms a bow and it is fixed and rigid. Opening and closing is effected by the movement of the posterior bar which has an L-shaped sclerotized lever with both dilator and occlusor muscles attached to it.

When ethylene dichloride was introduced to a chamber containing a resting beetle with the third spiracles closed the second spiracles stayed open all the time whereas the third spiracles opened but closed when fresh air was readmitted. Thus the action of ethylene dichloride is reversible. Ethylene dichloride always caused the second and third spiracles to open. Whenever the spiracles opened, they remained open until the beetle was exposed to fresh air. Tests were also done with adult *Blattella germanica* (L.). Both first and second spiracles possess an occlusor muscle and opening is effected by the elastic nature of the spiracular closing, the roaches showed much excitation and there was rapid fluttering

of both spiracles.

Only the third spiracle was used in isolation because it remained closed after isolated. Variable results were obtained. The responses were slow, for example one spiracle only started to open 5 minutes after ethylene dichloride was introduced and 25 minutes later it was only open half-way.

In order to see how the spiracles would respond to ethylene dichloride when only the central nervous system was treated, the ventral nerve cord was exposed by dorsal approach and ethylene dichloride was applied to the anterior end of the ventral nerve cord in the prothorax with a very small fumigant soaked cotton wad. In all tests, both the second and third spiracles opened in response. To see if application of ethylene dichloride to the peripheral nerves would result in similar changes, the tarsus of an insect was brought into contact with a small cotton wad moistened with fumigant, but this failed to cause the spiracles to open. Instead, both second and third spiracles showed repetitive fluttering.

When the beetles were treated with carbon disulphide, the second spiracles always opened but no consistent results were obtained with the third spiracles. The responses of the spiracles in one individual after carbon disulphide was introduced were studied in greater detail. The second spiracle, once it had responded to the fumigant by opening, remained open even after it was exposed to fresh air. The third spiracle closed after carbon disulphide was introduced into the chamber but opened after exposure to fresh air. It closed again when carbon disulphide was readmitted. This reversibility as found in ethylene dichloride shows the narcotic nature of the two compounds. When *Blattella germanica* were similarly treated, in all four tests the first two spiracles closed when paralysis took place. No consistent results were obtained when carbon disulphide was applied to isolated spiracles.

When carbon disulphide was applied locally to the ventral nerve cord, both the second and third spiracles opened as long as the cotton wad remained in contact, but the third spiracle resumed normal movements shortly after the cotton wad was removed. Application of carbon disulphide to the tarsus only caused some excitation of the beetles and more rapid movements of the spiracles.

#### **Effects on the Ventral Nerve Cord and Muscle**

To obtain further evidence of the effects of carbon disulphide and ethylene dichloride on the electrical activity of the ventral nerve cord, male *Periplaneta americana* were used. The ventral nerve cord of roaches which had been paralysed by ethylene dichloride or carbon disulphide, did not show the spontaneous activities detected in the control specimens. Spontaneous activity began to appear shortly before the roaches started to stir. But local application of these fumigants to the ventral nerve cord with a micro-syringe produced repetitive discharges.

In the studies on spiracular movements, muscle contractions are involved. Further evidence was obtained by perfusing one microlitre of either fumigant into an isolated leg of *Periplaneta americana* with a micro-syringe. The coxa and femur were flexed together and they remained

in that state for 1.5 hours when observation stopped. The same was found with femora and tibiae of isolated legs of *Tenebrio molitor* adults when the cut ends of the legs were brought into contact with a small cotton wad soaked with the fumigant.

When isolated legs of adult *Tenebrio molitor* were put in a petri dish and ethylene dichloride was injected into the dish, the femora and tibiae were flexed together in 35 seconds after ethylene dichloride was introduced. On exposure to fresh air, they gradually extended. The same results were obtained with isolated legs treated with carbon disulphide except that flexing occurred in 25 seconds.

It was noted before that after 5 hours of fumigation with ethylene dichloride, the bodies of many larvae of *T. molitor* became flaccid, some died within 5 days, but some survived beyond that period. In the latter, ethylene dichloride seemed to cause some permanent injury either to the nerves or to the muscles for many of them never regained their locomotive power and one of them molted to the next instar the second day after treatment but was unable to shed the old cuticle.

## DISCUSSION

Carbon disulphide had no effect on oxygen consumption by *Tenebrio molitor* adults either during or after treatment. Although there was an increase of oxygen consumption by *Tenebrio molitor* larvae during treatment with carbon disulphide, this increase did not persist after the treatment was ended. It is suggested that there was only sorption of carbon disulphide by the insect tissues during the treatment. This is confirmed by the increase of weight of insects during treatment and agrees with the observations of Shafer (1911) and McKee *et al.* (1943) that insects and vertebrate tissues can become saturated with carbon disulphide. Shafer (1911, 1915) found that carbon disulphide inhibited oxygen consumption by living *Passalus cornutus* but reanalysis of his data in the earlier paper shows that there was no significant difference between the control and the treated specimens and also that there was no significant difference in respiratory quotients between them. In his later paper Shafer (1915) used low, high, and nearly saturated concentrations. When a low concentration was used, in 29 hours, the oxygen consumed was 5.5 cc by the two treated insects and it was 6.4 cc by the two control insects. It is hard to say whether the difference is significant. In high and nearly saturated concentrations, the controls used 6 - 16 times more oxygen than the treatments. With these high concentrations, the insects probably only survived a few hours and not as long as the period during which the oxygen consumption was measured (16 - 24.5 hours). My data agree reasonably well with Shafer's (1911) data in that there was no significant difference between the oxygen consumption by the control and by the treated insects when active insects were treated with lower doses. However, I found that when insects were first anaesthetized with chloroform, the control specimens consumed more oxygen than the treated. That the unanaesthetized carbon disulphide treated insects did not show a decrease in oxygen consumption was probably because this was offset by an increase



in oxygen consumption because of muscular contractions as exemplified by the folding of the legs. Since the legs of the adults anaesthetized with chloroform were also folded indicating tetanic muscular contraction, the muscles of the treated and the control insects were in the same state and only then the intrinsic effect of carbon disulphide could be seen. The data obtained with homogenized tissues confirm the data obtained with anaesthetized insects and also confirm the observations of Shafer (1915) using tissue extract of *Passalus cornutus*. I found that the extent of decrease of oxygen consumption in the treated samples depends on carbon disulphide concentration, inhibition being greater in adults than in larvae. The present data do not agree with those obtained with rabbit tissue by De Meio and Brieger (1949).

No previous work has been done on the effect of ethylene dichloride on respiration. The present work with active insects indicates very clearly that ethylene dichloride causes an increase in oxygen consumption and that there is some correlation between oxygen consumption and the activities of the treated insects. Ethylene dichloride did not increase tissue respiration but rather the effect is through the action on activities. Studies with homogenized tissue showed that a lower dose of ethylene dichloride did not affect oxygen consumption significantly, but a higher dosage did decrease oxygen consumption. The cause of inhibition of oxygen consumption by higher doses of ethylene dichloride is not known but these results correspond well with the finding (Winteringham & Hellyer 1954) that longer exposure of *Musca domestica* caused considerable depletion of ATP and arginine phosphate. Insects paralysed by ethylene dichloride showed no decrease in oxygen consumption although it is expected that cessation of activities would be accompanied by such a change; probably contraction of muscles caused by these fumigants after paralysis accounts for this maintained rate of oxygen consumption. No difference was found in oxygen consumption of the anaesthetized treated and control specimens, the reason being that the muscles of the treated and control were in about the same state of contraction.

Ethylene dichloride resembles many contact insecticides such as chlorinated hydrocarbons, dinitro compounds, nicotine, pyrethrin, and organic phosphates which cause an initial increase of respiration and then a decrease towards the normal level, and these correlate with initial excitation and eventual paralysis of the treated insects (Harvey & Brown 1951).

In pyrethrins poisoning, the initial excitatory phase has been attributed to the stimulation of the peripheral sensory nerves (Hutzel 1942 a, b, Page *et al.* 1949). The larvae of *Tenebrio molitor* treated with ethylene dichloride developed symptoms similar to those of caterpillars poisoned by a median lethal dosage of pyrethrins (Brown 1951). The convulsions which succeed the initial excitatory phase in pyrethrin poisoning are attributed to stimulation of the central nervous system and the progressive paralysis is attributed to the onset of pathological changes in the nervous system (Brown 1951). Lowenstein (1942) found that under the influence of pyrethrins, the initial excitatory phase was marked by a massive discharge of a number of impulses and that a spontaneous synchronized discharge of continuous trains of giant-fibre potentials became



prominent. It is possible that ethylene dichloride acted essentially in the same way as pyrethrins. There is evidence that ethylene dichloride caused initial excitation of the ventral nerve cord, since the insects were always in a state of excitation after the application of this chemical and prior to paralysis. Although it has been shown that local application of ethylene dichloride and carbon disulphide to the ventral nerve cord caused an increase in spontaneous nervous activity, this could be due to the contact action of the cotton wool on the ventral nerve cord.

McGovran's (1932) finding that carbon disulphide increased the average rate of tracheal ventilation of the grasshopper *Arphia sulfuræ* (Fab.) in the first five minutes may be disputed because of his technique. He confined the thorax in a small chamber containing carbon disulphide with abdomen in a separate chamber containing air. The decrease in pressure of the chamber containing the thorax was taken as the amount of air ventilated from the first chamber through the thorax and abdomen to the second chamber, preventing him from distinguishing between sorption of carbon disulphide and ventilation. Insect and vertebrate tissues quickly become saturated with carbon disulphide as has been shown here and previously by McKee *et al.* (1943) and Shafer (1944). Ethylene dichloride certainly increased the rate of ventilation before the insects were paralysed since hyperactivity demands more oxygen and the wriggling movements of the larvae are likely to increase ventilation. It was demonstrated here that ethylene dichloride, but not carbon disulphide, caused an increase in abdominal ventilation movements in *T. molitor* adults before they were paralysed.

Carbon disulphide acts faster than ethylene dichloride. This can be attributed to the fact that carbon disulphide vapour has a greater penetrating power (Sun 1947) since it has a lower molecular weight and it may depress or abolish the peripheral nerve potential and conductivity as found in Japanese toad *Bufo vulgaris japonicus* (Echikawa 1959a). The fact that ethylene dichloride was as quick as carbon disulphide in paralysing adults may be due to its effect on the spiracles, since both second and third spiracles were completely opened during fumigation with ethylene dichloride. In the larvae, however, all spiracles were closed and they showed no visible movements.

When the anterior part of the ventral nerve cord was treated with either fumigant, the spiracles always opened. However, when carbon disulphide was applied in vapour form to the whole insects, variable results were obtained. It seems unlikely that the response of the spiracle depends on the local concentration of carbon dioxide, for when isolated spiracles are exposed to carbon disulphide vapour, carbon dioxide can easily diffuse out.

Echikawa (1959b) found that the skeletal muscle fibres of the toad were non-reactive to carbon disulphide, but the motor end-plates showed spontaneous activity after treatment. When skeletal muscle was induced to contract by carbon disulphide, it would remain in such a state for a long time, although fatigue of the motor end-plate occurred readily in the presence of carbon disulphide. External force was required to stretch the muscle. A similar phenomenon was observed with muscles of isolated legs of both *Periplaneta americana* and *Tenebrio molitor* when they were perfused

with, or treated with the vapour of, either carbon disulphide or ethylene dichloride. These fumigants probably act on motor end-plates in insect muscles as in the toad. If carbon disulphide and ethylene dichloride can really act on the motor end-plates in spiracular muscles they can cause both the dilator muscle and occlusor muscle to contract, and it seems that it is the net result of these forces that cause the third spiracle to open or to close. Which of the two muscles exerts a greater force might depend on physiological conditions.

When whole insects were treated with ethylene dichloride vapour, the third spiracle always opened. The difference of responses given by intact and isolated spiracles seems to suggest that the ventral nerve cord was responsible for the consistent opening of the third spiracle in the presence of ethylene dichloride vapour. Miller (1960b) found that in the desert locust, *Schistocerca gregaria* (Forsk.), some spiracles have antagonistic muscles as in the third spiracle of *Tenebrio molitor* and two different types of action potentials are involved for their movement. Usually, only one type of action potential could be recorded from the transverse nerve and only one of the muscles is functioning all the time. In *Tenebrio molitor* judging from the structure of the third spiracle, opening of the spiracle needs active contraction of the dilator muscle and relaxation of this muscle would bring the valve back to the closed position. The occlusor muscle is probably only used for active closing. It is suggested that when the ventral nerve cord produced massive discharges in ethylene dichloride only one type of action potential was produced and so tetanic contraction only occurred in the dilator muscle.

These results point to the importance of spiracular structure. For example, if all the spiracles have only dilator muscles, then during fumigation they would all open and facilitate the entrance of the fumigant. Insects with only occlusor muscles to the spiracles, would have these all closed during fumigation. This importance of spiracular structure has been pointed out by Sharplin & Bhambhani (1963) in their study of spiracular structure and water loss under reduced pressure. The responses of the spiracles depend on their structure and the nature of the fumigants, having no essential relation to the effects of fumigants on respiration.

Carbon disulphide and ethylene dichloride are narcotics but narcosis is not the cause of death of insects (Brown 1951). Hurst (1945) thought that narcosis may involve the indirect blocking of enzyme activity by the adsorption of insecticides on the protective lipo-protein components of the nervous tissue. The narcotics are known to inhibit respiratory enzymes (Shafer 1911, 1915, McKee *et al.* 1943, Anonymous 1949, Baldwin 1952) but ethylene dichloride has not been shown to have such an effect. Fukami *et al.* (1959) showed that there is a positive correlation between the action of rotenone on nerve conduction and inhibition of respiratory metabolism; the rotenone derivatives which have a potent inhibitory action on metabolism block nerve conduction. It seems very likely that the cause of inhibition of nerve conduction in peripheral nerves of the toad by carbon disulphide (Echikawa 1959a) is the inhibition of the succinic oxidase enzyme system which is important in normal nerve tissue metabolism (McKee *et al.* 1943). If this is true, then carbon disulphide might

also interfere with insect peripheral nerve conduction.

In conclusion, ethylene dichloride increased the oxygen consumption by larvae but not adults; it had a very slight effect on larval tissue homogenate but only very high doses had an effect on the oxygen consumption by adult tissue homogenate. Carbon disulphide had no effect on oxygen consumption by normal insects but the oxygen consumption by anaesthetized insects was depressed. Tissue homogenate was affected by carbon disulphide, the extent of depression of oxygen consumption depending on the dosages applied. Although both ethylene dichloride and carbon disulphide were taken up by insect tissue during fumigation, sorption occurred more quickly in carbon disulphide, due to the lower molecular weight and hence higher penetration speed. The increase in abdominal ventilation movements caused by ethylene dichloride, is probably due to its stimulating effect, causing hyperactivity of the insects.

The larvae were paralysed by carbon disulphide much more quickly than by ethylene dichloride and this again is related to the difference in molecular weight and hence penetrating speed of these two fumigants. In adults, the greater molecular weight of ethylene dichloride was compensated for by its effect on ventilation and the spiracles, so that both of these fumigants paralysed the adults in about the same time.

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## CORRIGENDA

- P. 224 (vol. II, no. 3). For *Chematospyche analis* (Banks), read *Cheumatopsyche analis* (Banks); for *Trianodes marginata* Sibley, read *Triaenodes marginata* Sibley; for *Leptocalla exquisita* (Walker), read *Leptocella exquisita* (Walker); for *Agapetus hessi* Leonard & Leonard, under ♂, for 0 read 1.



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# Quaestiones entomologicae

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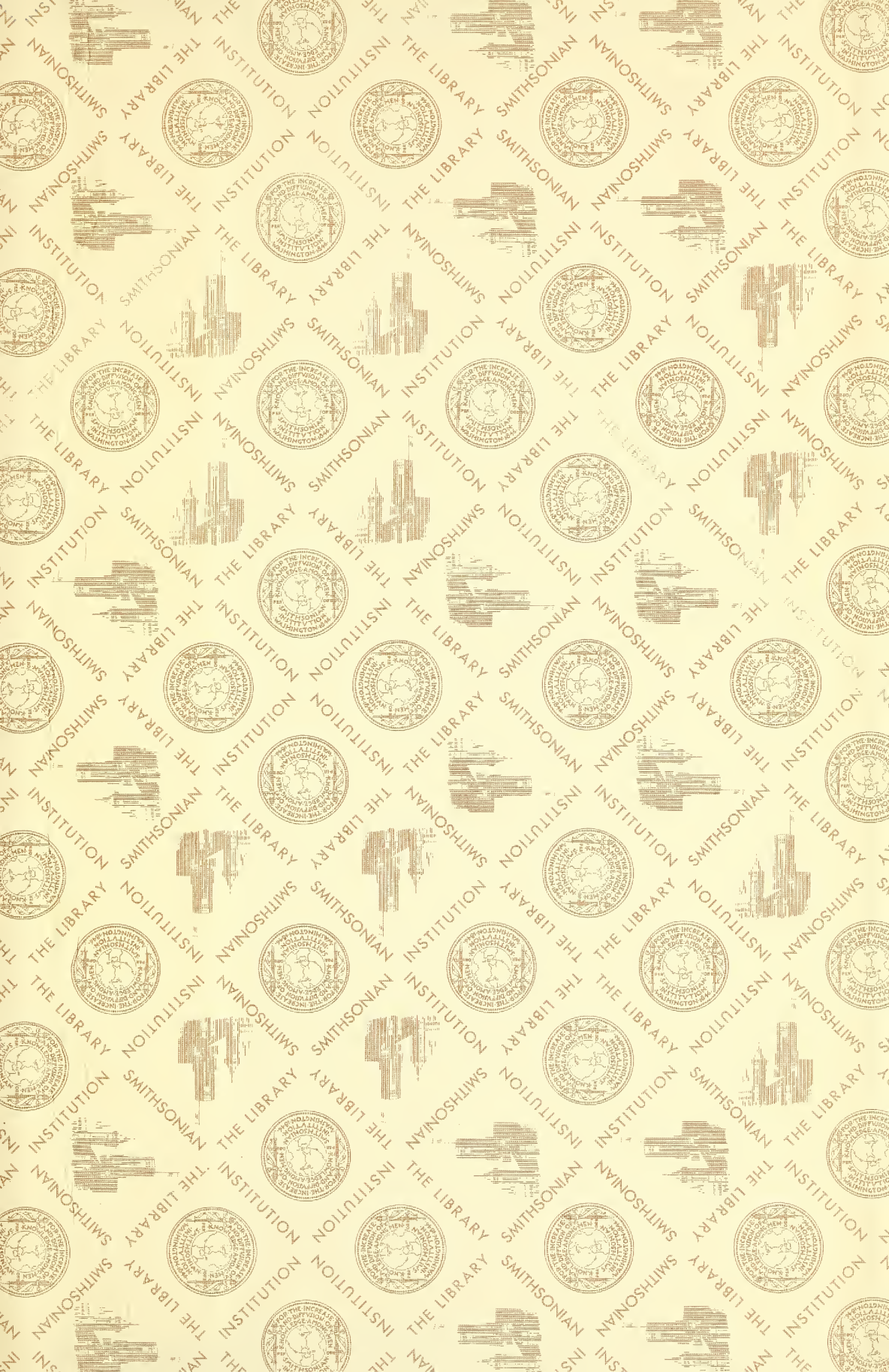


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